

# Additions and Corrections to the Taxonomy of the genus *Peasiella* Nevill, 1885 (Gastropoda: Littorinidae)

David G. Reid

Department of Zoology  
The Natural History Museum  
London SW7 5BD, UK  
D.reid@nhm.ac.uk

Yiu-Ming Mak<sup>1</sup>

Department of Ecology and  
Biodiversity  
The University of Hong Kong  
Hong Kong

## ABSTRACT

*Peasiella* is a genus of the Littorinidae with minute, trochoidal shells, found only in the Indo-West Pacific region. A previous monograph recognized six Recent species. As a result of new anatomical information (reproductive anatomy, egg capsules, radulae) two of these are divided into five and two species, respectively, to make a total of 11 species in the genus. Three of these are described as new. Additional notes on distribution, variation and nomenclature are provided on other species. Characters of the radula and pallial oviduct are relatively uniform throughout the genus, but penial shapes are often diagnostic. Shell shape and sculpture show extreme intraspecific variability.

## INTRODUCTION

*Peasiella* is one of the more poorly known genera of the Littorinidae. In common with all members of the subfamily Littorininae, its species occur on hard substrates in the littoral zone. Although easily accessible and often abundant, they are infrequently collected owing to their small size and cryptic habit in rock crevices and among oyster and barnacle shells. All known species occur in the Indo-West Pacific province and most are entirely tropical, although several extend into the temperate zones of southern Africa and the northwestern Pacific. Among littorinids, they are readily recognized by their small (1–7 mm diameter), trochoidal or depressed shells, lacking spines, with open umbilicus and multispiral operculum. These characters are superficially similar to those of trochids (but lacking the nacreous interior of that group), with which they were often confused by early authors (see review of taxonomic history by Reid, 1989a). Other littorinids with trochoidal shells include the genera *Bembicium* and *Risellopsis* from Australia and New Zealand (Reid, 1985), and *Tectarius* and *Cenchritis* from the Indo-West Pacific and western Atlantic (Rosewater, 1972; Reid, 1989b; Reid & Geller, 1997).

For long these small littorinids were neglected taxonomically. The most recent monograph of extant and some fossil *Peasiella* species was that by Reid (1989a); before this the only compilations were a list by Nevill (1885) and a monograph by Tryon (1887). The anatomy (male and female reproductive tracts, paraspermatozoa, egg capsule, alimentary tract, head-foot pigmentation), radula, protoconch and teleoconch were described in detail by Reid (1989a). As a result, the genus was defined not only by shell and opercular characters, but also by the unique combination of the elongate penis with single mamilliform penial gland and closed vas deferens, together with the double-looped form of the pallial oviduct, and other anatomical features. These same characters were included in a phylogenetic analysis of the morphology of the genera and subgenera of the Littorinidae (Reid, 1989b). However, since none of the coded anatomical characters appeared to be apomorphic within the family, the only formal synapomorphies of the genus in this analysis were the trochoidal shell shape and multispiral operculum, and neither of these was unique. Nevertheless, the close morphological similarities among its members leaves little doubt that the genus is a monophyletic one; the arrangement of the loops of the pallial oviduct is one unique character, but owing to difficulties of coding such structures it did not appear as such in the formal analysis. As a result of Reid's (1989b) phylogenetic analysis, it was clear that *Peasiella* was a member of the derived subfamily Littorininae, and probably a relatively basal member, although its precise relationships with such genera as *Maimocaringia*, *Cenchritis* and *Tectarius* were not resolved. A recent molecular study included a species of *Peasiella*, with members of *Tectarius*, *Cenchritis* and *Nodilittorina*, but did not find any close relationships with these other genera (Reid & Geller, 1997).

In the previous systematic account of *Peasiella* species (Reid, 1989a), anatomical details were provided for all the six species then recognized. However, the amount of material available was limited; for example, for *P. isseli* only one preserved male was dissected, and for *P. infracostata* only seven. As a result, it was concluded

<sup>1</sup> Present address: 13/F, Canton Road Government Offices, Agriculture and Fisheries Department, Hong Kong

that the genus was anatomically rather uniform, without the striking differentiation in reproductive characters that has proved so useful for the discrimination of species complexes elsewhere in the family (e.g. Reid, 1986a, 1988, 1996). Instead, it was necessary to base species definitions largely on the shape, sculpture and color of the shell (although these characters were evidently variable), and on geographical distributions. Anatomical characters such as head-foot pigmentation, the number of cusps on the outer marginal radular tooth, and presence or absence of a copulatory bursa provided only minor input.

Our attention was once more drawn to the systematics of *Peasiella* as a result of a study by one of us (Y-MM) of the littorinids of Hong Kong. The fauna of Hong Kong was thought to include three *Peasiella* species (Reid, 1992), the highest number then known to occur sympatrically. However, it was found that two distinct shell forms of *P. 'infracostata' sensu* Reid (1989a), both rare in Hong Kong and not yet found syntopically (i.e. on the same shores), produced egg capsules of different shape. This prompted a reexamination of this supposed species throughout its wide range in the Indian and Pacific Oceans. Meanwhile, further collections were made by Y-MM throughout the Far East. During the past decade much new material has also accumulated in the major museums. Using this new material, we found that penial form was, after all, a character showing useful interspecific variation. As a result, we have revised the taxonomy of two species complexes; *Peasiella 'infracostata' sensu* Reid (1989a) is here shown to consist of five species, and *P. 'isseli' sensu* Reid (1989a) of two. These seven species are fully described. We also record additional information on the variability, distribution and nomenclature of other *Peasiella* species. The number of species recognized in the genus is therefore increased from six to eleven.

## MATERIALS AND METHODS

The descriptions and records are based on material in the following museums: Natural History Museum, London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Instituut voor Systematiek en Populatiebiologie, Amsterdam (ZMA); Nationaal Natuurhistorisch Museum, Leiden (NNML); Institut Royal des Sciences Naturelles de Belgique (IRSNB); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University (MCZ); Los Angeles County Museum of Natural History (LACM); Natal Museum (NM); National Science Museum, Tokyo (NSMT); Department of Earth and Planetary Science, Kyushu University (KU); Australian Museum, Sydney (AMS) and the private collections of H. Dekker, The Netherlands (HD) and J. Le Renard, Paris (LR). In addition, type specimens have been examined from Oxford University Museum (OUM); Museo Civico di Storia Naturale 'Giacomo Doria', Genoa

(MGD) and Zoological Survey of India, Calcutta (ZSI). Unless otherwise indicated, all figured specimens are in BMNH. Lectotypes have been designated from syntypic series only for valid species names.

Shell height (H) was measured parallel to the axis of coiling, and maximum shell diameter (D) perpendicular to this axis. The height/diameter ratio was used as a simple index of shell shape. The number of whorls of the protoconch was counted as described by Reid (1996: 9). Where counts of the number of ribs above the periphery are given, this includes the strong rib at the periphery; this rib is not included in counts of the basal ribs. Living material was preserved in 80% ethanol, and dissected under a binocular microscope. Pallial oviducts were examined by dissection; in very small animals the copulatory bursa can be impossible to find unless filled with recently deposited sperm; to confirm absence of the bursa would require histological preparation, but this was not done in the present study. The loops of the albumen and capsule gland follow a similar path in all species examined, and are therefore not re-described (see Reid, 1989a, for description and figures). Radulae were cleaned of tissue in a cold, dilute solution of hypochlorite bleach, thoroughly rinsed in distilled water, and mounted on a thin layer of polyvinyl acetate glue on glass cover slips. Radulae were examined with a scanning electron microscope. Unworn radular sections were photographed from three orientations: vertically above flat radula (to show shape of teeth), at an angle of 45° from front end of radula (to show shape of tooth cusps), and at an angle of 45° from the side of the radula (to show relief). For three species, egg capsules were obtained from living animals. Females were placed individually in plastic vials (20 × 47 mm) half filled with filtered seawater. Vials were covered and kept at room temperature (24–26° C) with no aeration. The water was renewed daily, and eggs were collected from the bottom of the containers. Eggs were preserved in 5% formalin in seawater, for subsequent examination and measurement using light microscopy.

The lists of material examined are those records used for the distribution maps. Numbers of specimens dissected are indicated by M (male), F (female); R indicates radula preparation, and P protoconch examination. For the seven species described in detail, the material listed includes that examined during the previous study by Reid (1989a), and the descriptions supersede the earlier account. This earlier work should still be consulted for detailed descriptions of the histology of the reproductive system and of the sperm. For those species for which only additional notes and records are given, full descriptions and other records can be found in Reid (1989a).

## SYSTEMATIC DESCRIPTIONS OF REDEFINED AND NEW SPECIES OF *PEASIELLA*

*Peasiella infracostata* (Issel, 1869)

(Figures 1–5, 35–41, 76–79, 108–109, 131)

*Trochus* sp. Andouin, 1826:42

*Risella infracostata* Issel, 1869:195–196, 348 [refers to Savigny,

1817: pl. 5, fig. 40.1, 40.2; lectotype (Reid, 1989a; fig. 41) + 3 paralectotypes MNHN, seen; Suez [Issel], Pallary, 1926:56, pl. 5, fig. 40.1, 40.2. Bouchet & Danrigal, 1982: 13, fig. 64.

*Risella* (*Peasiella*) *infracostata*.—Nevill, 1885:160. Tryon, 1887: 264, pl. 50, figs. 41, 42.

*Peasiella infracostata*.—Reid, 1989a:61–64, figs. 106–109, 112 [in part; includes *P. fasciata*, *P. fuscopiperata*, *P. habei*, *P. patula*]. Bosch *et al.*, 1995:46, fig. 118.

? *Risella* (*Peasiella*) *tantillus* var. *subinfracostata* Nevill, 1885: 160 [lectotype (Reid, 1989a; fig. 35) + 2 syntypes ZSI; lectotype seen; Nicobar Islands].

**Nomenclature:** In his description of this species, Issel (1869) referred to Savigny's (1817) unlocalized figures of Egyptian material, and also mentioned three specimens of his own from Suez; the latter were not found by Bouchet & Danrigal (1982) in Issel's collection in MGD. Reid (1989a) therefore designated one of four shells in the Savigny Collection in MNHN as the lectotype.

The identity of *Risella* (*Peasiella*) *tantillus* var. *subinfracostata* Nevill, 1885, is uncertain. The lectotype (Figure 35) measures 2.3 mm in diameter by 2.2 mm in height (H/D 0.96), is almost smooth above the periphery, but for fine spiral microsculpture and traces of about four spiral grooves near the periphery; the base bears four subequal ribs around a small umbilicus; the color is cream with a single brown spiral line on the first whorl of the teleoconch, and no other pattern. Of the known species of the genus, this shell can be compared with *P. infracostata* and *P. fasciata*. In outline it resembles *P. infracostata*, for the whorls and aperture are less rounded than in *P. fasciata*; however, it lacks the enlarged mid-basal rib that is often present in the former. The sparse color pattern is unlike any known specimens of either of these species. The locality of Nevill's shells, from the Nicobar Islands, is far from the closest known occurrence of *P. infracostata* in Bombay, and from that of *P. fasciata* in Borneo. The only other *Peasiella* species recorded from the Andaman Sea is *P. roepstorffiana* (Reid, 1989a), but that species usually has stronger spiral sculpture, flatter whorls and a strong peripheral keel. Until more information is available, the name is tentatively included in the synonymy of *P. infracostata*.

Reid (1989a) confused five species under the name *P. infracostata* (here distinguished as *P. infracostata* s.s., *P. fasciata*, *P. fuscopiperata*, *P. habei* and *P. patula*), misled by their similar and confusingly variable shells.

**Shell (Figures 1–5, 35–41):** Adult size range 1.1–2.6 mm diameter. *Shape:* thickness varies from delicate and

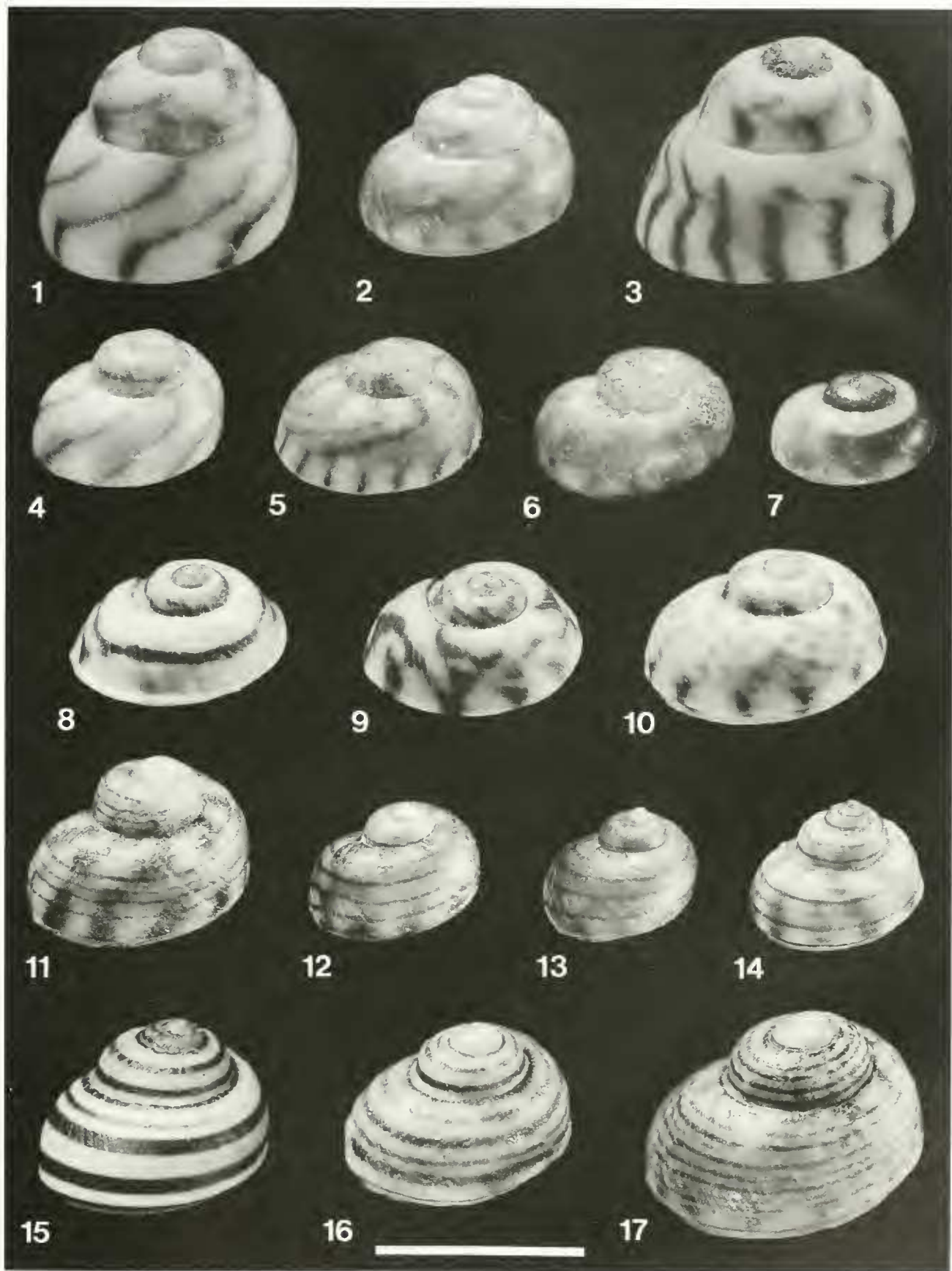
translucent, to thick-walled and opaque; equilaterally conical to depressed-globular (H/D 0.7–1.0); outline domed; whorls usually rounded or with rounded shoulder, becoming almost flat-sided on last whorl of largest, thick-walled shells; suture always distinct; periphery occasionally uniformly rounded, but usually marked by sharp angle or rib, rarely developed as a narrow flange; base usually slightly rounded, becoming flat or even slightly concave in largest, thick-walled shells; umbilicus small to large, occasionally closed in thick-walled shells; columella narrow, uniformly rounded. *Sculpture:* protoconch not seen, apex usually eroded; teleoconch whorls always lacking ribs above periphery, microscopically smooth or with fine spiral microstriae (rarely, about 6 striae may be more prominent, but not developed into ribs, Figure 39); 1–4 ribs on base (rarely absent, or 5–6), of which that at mid-point of radius is usually most prominent (producing slight angulation of base). *Color:* translucent yellow-brown, opaque white where shell is thicker at suture and periphery (entirely white in thick-walled shells); pattern of pale or dark brown or black, oblique or zigzag, narrow lines from suture to periphery, numbering 5–19, darkest at periphery and sometimes also at suture; pattern occasionally represented only by peripheral stripes; spire may be brown, or frequently marked only by single spiral brown line; base usually pale with brown line in outermost groove, line sometimes absent, base rarely brownish with paler ribs; columella and parietal area usually not colored, rarely brown.

**Animal:** *Head-foot:* front of head blackish, with a separate black band across base of snout; tentacles unpigmented; foot may have black pigment around operculum. *Penis* (Figures 76–79): filament long (50–60% total length), tapering; base slightly thicker, with single small manilliform penial gland. *Pallial oviduct:* bursa not seen. *Radula* (Figures 108, 109): cusps pointed, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 6–7 long, pointed cusps, outermost more rounded, becoming smaller toward midline.

**Distribution:** *Habitat:* Among barnacles in upper eulittoral on surf beach (Oman; J. D. Taylor); rock pool on limestone, in upper eulittoral of sheltered shore (Oman; E. Glover); under rocks and stones in intertidal (Oman; R. G. Moolenbeek & H. Dekker); under coral blocks in eulittoral (Egypt; D. G. Reid). Abundant at some localities in Oman and at Karachi, but elsewhere appears to be scarce.

→

**Figures 1–5.** *Peasiella infracostata*. 1. Ras al-Hadd, Oman (BMNH 1996381). 2, 4. Karachi, Pakistan (BMNH 1996383). 3. Tiwi Beach, 30 km S Mombasa, Kenya (BMNH 1996384). 5. 4 km S Ras Qudufah, Masirah I., Oman (BMNH 1996385). 6–10. *Peasiella fuscopiperata*. 6. Lectotype of *Cyclostrema fuscopiperata* Turton, 1932, Port Alfred, South Africa (OUM). 7. North Bay, Benguera I., Mozambique (NM K7412). 8–10. Tiwi Beach, 30 km S Mombasa, Kenya (BMNH 1996386). 11–13. *Peasiella patula*. 11. Holotype, Changi Point, Singapore (BMNH 1996276). 12, 13. St. John's I., Singapore (BMNH 1996387). 14–17. *Peasiella fasciata*. 14. Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). 15. Holotype, Turtle Bay, Cape Ferguson, Queensland, Australia (BMNH 1996272). 16, 17. Cape d'Aguiar, Hong Kong (BMNH 1996388). Scale bar = 2 mm.



*Range (Figure 131):* East Africa, Red Sea, Oman, Pakistan, possibly Nicobar Islands.

*Records and material examined:* Moçambique: Conducia Bay (NM). Tanzania: Zanzibar (BMNH). Kenya: Tiwi Beach, 30 km S Mombasa (BMNH, 2M). Somalia: Mogadiscio (ANSP). Egypt: Hurghada (BMNH; HD); Suez (Issel, 1869). Yemen: Périm Island (MNHN); Aden (MNHN); Hawf, al-Mahrah (IID). Oman: Raysut, Salalah (BMNH; ZMA); Kuria Muria Islands (ZMA); Masirah Island (BMNH, 2M, 1F; ZMA); Ras al-Hadd (BMNH, 1M, 1F, 1R). Pakistan: 7 km W Bulegi Point, Sind (LACM); Karachi (BMNH, 3M, 5F, 2R). India: Mada Island, Salsette Island, Bombay (ANSP); Nicobar Islands (ZSI; uncertain identification, see Nomenclature, above).

**Remarks:** The shell of this species shows considerable variation in shape, thickness, opacity and coloration. Thin-walled, translucent shells with indistinct pattern, rounded whorls and no peripheral rib (Figures 2, 36, 40) look very different from larger, thick-walled, opaque, strongly domed shells with striking black and white pattern, sharply angled periphery and flat or concave base (Figures 1, 3). Yet these extremes are connected by many intermediates, and even within samples from a single locality there can be great variation (Figures 36, 37, 39, 40). Whether there is a geographical or ecological correlation to this variation is not clear. Shells from Pakistan are mostly of the translucent form with pale pattern, those from East Africa are opaque and strongly marked, whereas those from the Red Sea and Oman span the entire range. A common feature of the shells is the generally small number of basal ribs, often 3 or less, of which that at the mid-point of the radius is usually slightly larger than the rest. The color pattern of narrow oblique or wavy axial lines is also a useful recognition character.

This species is closely similar in shell characters to *P. fuscopiperata*, and some of the translucent, rounded shells are indistinguishable. That they are indeed distinct species is confirmed by the difference of the penis in each (long filament and small mamilliform gland in *P. infracostata*, short filament and large gland in *P. fuscopiperata*), which is maintained in syntopic samples from Tiwi Beach, Kenya (Figures 76, 77, 80, 81). At this locality (as in a dry collection from Conducia Bay, Moçambique) both species are represented by thick-walled forms; the shells of *P. infracostata* have a taller spire, more steeply domed, with flatter final whorl and sharper

peripheral angle, the base is flatter with 1–2 or rarely 3 coarser ribs (3–4 in *P. fuscopiperata*) and the umbilicus smaller or closed; the color pattern is sometimes very similar, but in *P. infracostata* the oblique lines are dark and more regular (Figure 3), whereas in *P. fuscopiperata* the coloration is much more variable in intensity and pattern, including irregular markings, spiral bands and fine marbling (Figures 8–10). Thinner-shelled forms of these two species are distinguished by the slightly taller spire of *P. infracostata*, and sometimes by the basal ribs, of which the central one is often enlarged in *P. infracostata*, whereas in *P. fuscopiperata* the ribs become larger toward the periphery.

As a consequence of this similarity, the southern geographical range of *P. infracostata* is uncertain. Available material from southern Moçambique and South Africa consists mainly of dry shells, of the translucent type. All anatomical material seen from this area has been of *P. fuscopiperata*, but more is required to confirm that *P. infracostata* does not occur. No anatomical material has been seen from the Red Sea (including the type locality, Suez), and the association of the name with the specimens from Oman and Pakistan is based on apparently identical shells and geographical proximity. The eastern limit of *P. infracostata* remains unclear; additional material is necessary to confirm the synonymy of Nevill's (1885) *subinfracostata* from the Nicobar Islands (see Nomenclature, above).

*Peasiella fuscopiperata* (Turton, 1932)

(Figures 6–10, 42–48, 80–83, 110, 111, 132)

*Cyclostrucma fuscopiperata* Turton, 1932:198–199, pl. 51, fig. 1379 [lectotype (here designated, 1.9 mm diam., Figure 6) + paralectotype, OUM, seen; Port Alfred, South Africa].

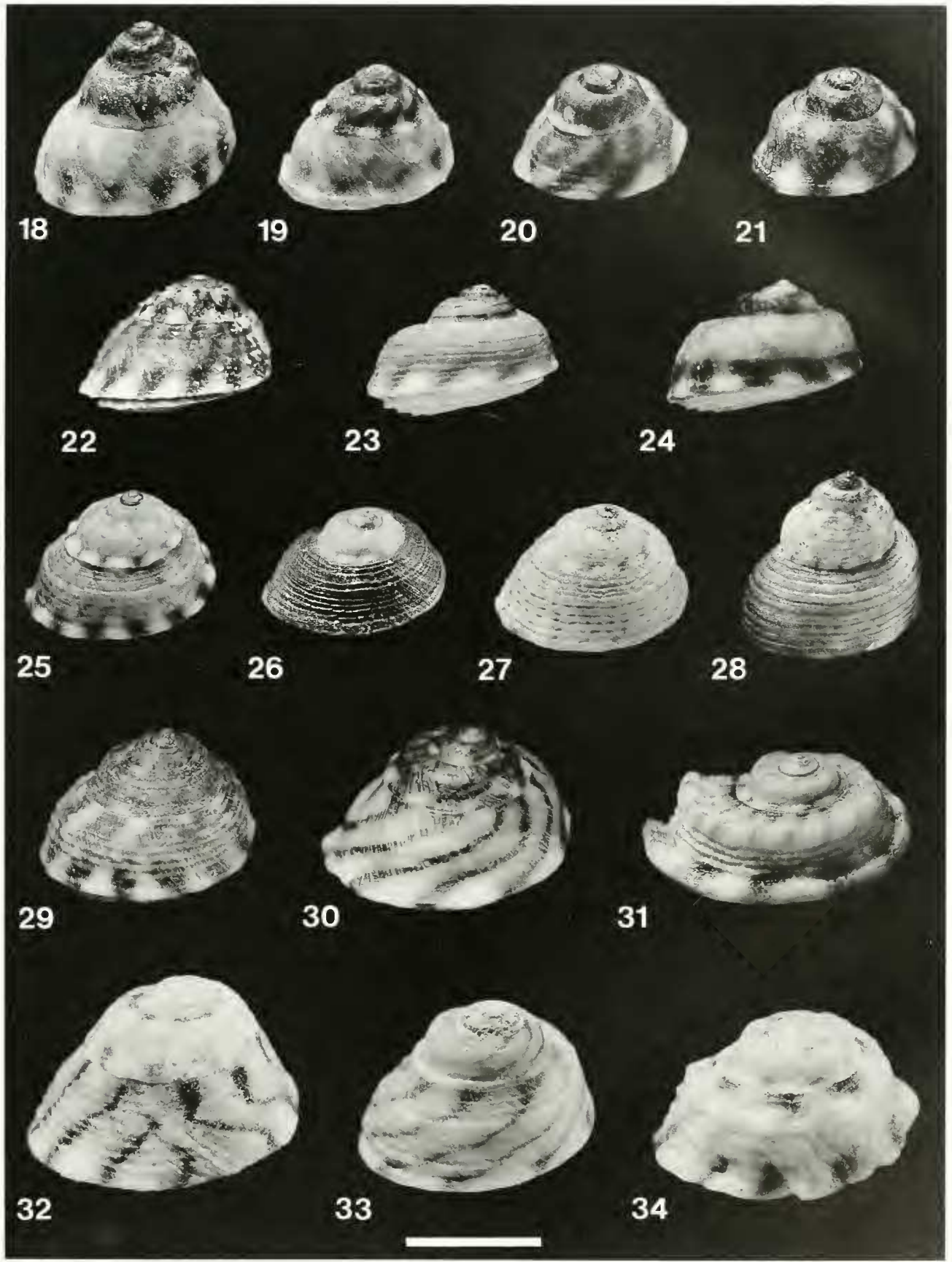
*Peasiella infracostata*.—Reid, 1989a:61–64 [in part; includes *P. infracostata*, *P. fasciata*, *P. habei*, *P. patula*; not *P. infracostata* (Issel, 1869)].

**Nomenclature:** Surprisingly, since this species is not uncommon in southern Africa, it does not appear to have been mentioned in works on mollusks of the region, except in Turton's (1932) original description of shells from the southern extremity of its range.

**Shell (Figures 6–10, 42–48):** Adult size range 1.3–2.7 mm diameter. *Shape:* thickness varies from delicate and translucent, to more solid and opaque; depressed to flattened (H/D 0.54–0.91); outline domed; whorls rounded, suture impressed; in thin-walled shells periph-

→

**Figures 18–24.** *Peasiella habei*. **18, 19.** 4–5 km SW Tsutsu, Tsushima I., Nagasaki Pref., Japan (BMNH 1996389). **20.** Holotype, Esu Cape, Shirahama, Wakayama Pref., Japan (BMNH 1996274). **21.** Tai Ping Bay, Qindao, China (BMNH 1996390). **22.** Lok Wo Sha, Hong Kong (BMNH 1996391). **23.** Baten, Okinawa, Japan (BMNH 1996392). **24.** Ma Liu Shi, Tolo Harbour, Hong Kong (BMNH 1996393). **25–29.** *Peasiella isseli*. **25, 28.** Dahiab, Sinai, Egypt (BMNH 1996394). **26, 27.** Hurghada, Egypt (BMNH 1996395). **29.** Suez, Egypt (BMNH 1882.8.7.316). **30–34.** *Peasiella mauritiana*. **30.** Lectotype of *Risella isseli* var. *mauritiana* Viader, 1951, Grand Bay, Mauritius (BMNH 1989004). **31.** Arabian Gulf (BMNH 1996396). **32.** Inhaca I., Moçambique (NM L3435). **33.** Sadli, Oman (BMNH 1996397). **34.** Zanzibar, Tanzania (BMNH 1904.10.20.97). Scale bar = 2 mm.



ery uniformly rounded or marked by slightly thickened rib only, in thicker shells periphery angled and marked by sharp keel or narrow flange; base rounded; umbilicus of moderate size; columella rounded, slightly thickened and angled at base. *Sculpture*: protoconch 240  $\mu\text{m}$  diameter, 2.5 whorls, protoconch 11 sculptured by scattered granules and narrow raised ridges (as in Figures 106, 107 of *P. fasciata*); teleoconch whorls usually microscopically smooth above periphery, or with fine spiral microstriae, rarely with 2–6 slight or indistinct ribs; 2–6 (rarely 0, 1 or 8) ribs on base, outermost strongest, becoming weaker toward umbilicus; basal ribs fine, indistinct or absent in thin-walled shells; rarely minute periostracal bristles present on basal and dorsal ribs. *Color*: thin-walled shells translucent pale yellow-brown with faint pattern of 6–14 oblique or wavy brown lines (sometimes present only as faint marbling), distinct only at suture and periphery; base unmarked; thicker shells opaque white or beige, with highly variable pattern: red-brown to black coarse, irregular pattern of bands, chevrons and zigzags, usually leaving an unpigmented sutural band; sometimes a continuous broad spiral band on shoulder; sometimes a paler brown pattern of diffuse marbling, with or without 9–12 darker peripheral spots; spire orange-brown, often with dark red-brown spiral band; base sometimes red-brown with 6–10 dark spots on white peripheral keel; lower columella and parietal callus sometimes red-brown.

**Animal:** *Head-foot*: front of head blackish, with a separate black band across base of snout; tentacles unpigmented; foot with some black pigment on sides or unpigmented. *Penis* (Figures 80–83): filament small (10–20% total length), tapering; base thicker, sometimes wrinkled, with single very large mamilliform penial gland occupying most of its length. *Pallial oviduct*: bursa not seen. *Radula* (Figures 110, 111): cusps pointed, major cusp of lateral and inner marginal tooth sometimes slightly rounded, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 5–8 long, pointed cusps, outermost more rounded, becoming smaller toward midline; base of rachidian tooth sometimes developing a pair of small posterior denticles.

**Distribution:** *Habitat*: Eulittoral; low, undercut limestone cliffs with fringing reef platform beyond (Kenya; D.S. Brown); alive in coralline algal debris washed up on strand line (South Africa; D. Herbert).

*Range* (Figure 132): East coast of South Africa to Kenya.

*Records and material examined*: South Africa: Port Al-

fred (NM, OUM); East London (NM); Mbotyi, Pondoland (NM); Port Edward (NM); Umdhloti, Natal (NM); Mapelane, Zululand (NM, 2M); Leven Point, Zululand (NM, 1M). Moçambique: Benguera Island, Bazaruto Archipelago (NM); Conducia Bay (NM). Kenya: Tiwi Beach, 30 km S Mombasa (BMNH, 7M, 4F, 4R, 1P).

**Remarks:** Reid (1989a) identified smooth-shelled forms of this species as *P. infracostata*, and those rare examples with spiral sculpture above the periphery as *P. isseli* (with which *P. mauritiana* was then included). The form of the penis provided the first evidence that this species is distinct; the short filament is found elsewhere in the genus only in *P. patula*, but there the mamilliform gland is of a different shape. The present species is sympatric with two others, *P. mauritiana* and *P. infracostata*, in East Africa, and penial shape is diagnostic of each. The shell is most similar to that of *P. infracostata*, and separation of the two has been discussed in the Remarks on that species. In both, the shell shows parallel variation in thickness, opacity, spire height, angulation of the margin and intensity of color pattern. Occasional shells with spiral sculpture above the periphery could be confused with those of *P. mauritiana*; *P. fuscopiperata* lacks the shoulder angulation of that species, is usually a more delicate shell and rarely shows the same pattern of strong oblique radial lines.

*Peasiella patula* new species

(Figures 11–13, 52–56, 84–87, 112, 113, 123, 127, 128, 133)

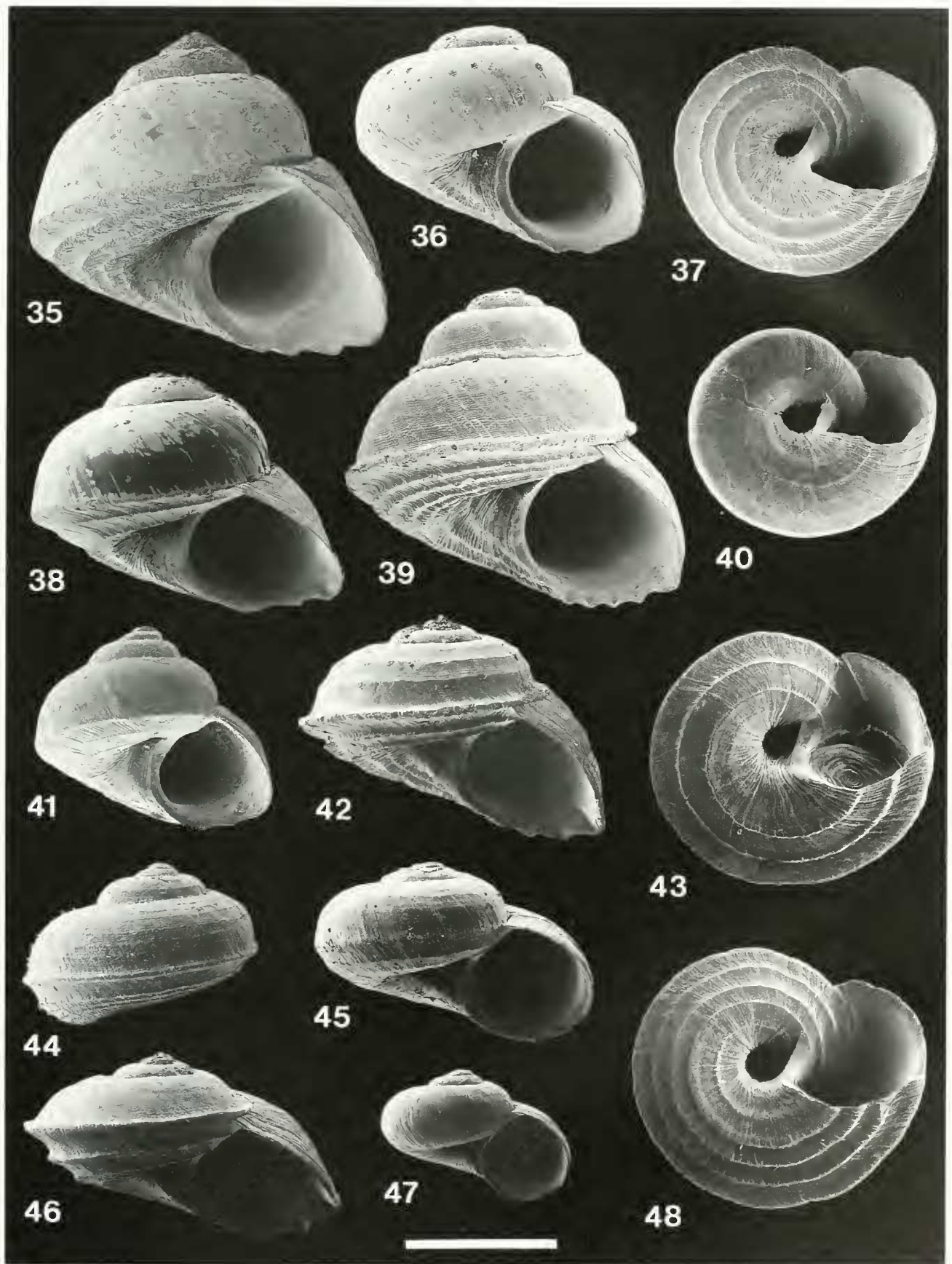
*Peasiella infracostata*.—Reid, 1989: 61–64, fig. 110 [in part; includes *P. infracostata*, *P. fuscopiperata*, *P. habeii*, *P. fasciata*; not *P. infracostata* (Issel, 1869)].

**Etymology:** Latin *patulus*, open, in reference to the relatively large aperture.

**Types:** Holotype BMNH 1996276 (Figure 11); 5 paratypes BMNH 1996277, 49 paratypes in alcohol BMNH 1996278 (Figures 87, 112, 113). Type locality: Changi Point, Singapore.

**Shell** (Figures 11–13, 52–56): Adult size range 1.2–2.0 mm diameter. *Shape*: depressed to conical (H/D 0.75–0.85); somewhat patulous, last whorl enlarged, aperture relatively large; protoconch (if present) projects as papillose tip to spire; whorls well rounded or inflated, often with rounded shoulder, suture impressed; angled periphery marked by sharp but barely projecting keel; base slightly rounded; umbilicus wide; columella narrow, curved at base; viewed from above or below, apertural

Figures 35–41. *Peasiella infracostata*. 35. Lectotype of *Risella* (*Peasiella*) *tantillus* var. *subinfracostata* Nevill, 1885, Nicobar Is (ZS1). 36, 37, 39, 40. Karachi, Pakistan (BMNH 1996383). 38. 4 km S Ras Qudufah, Masirah I., Oman (BMNH 1996385). 41. Lectotype of *Risella infracostata* Issel, 1869, Red Sea (MNHN). 42–48. *Peasiella fuscopiperata*. 42, 43, 46, 48. Tiwi Beach, 30 km S Mombasa, Kenya (BMNH 1996386). 44. Leven Point, Zululand, South Africa (NM E2745). 45. Mzamba, Transkei, South Africa (NM 3025). 47. Mapelane, Zululand, South Africa (NM D2415). Scale bar = 1 mm.





edge is curved (i.e. growing edge is prosocyr). *Sculpture*: protoconch 260  $\mu\text{m}$  diameter, 2.7 whorls, sculpture not preserved; teleoconch whorls smooth or with 6–7 indistinct to strong spiral ridges; 4–5 fine ribs on base; surface smooth or with fine spiral microstriae; basal ribs occasionally bear minute periostreal bristles. *Color*: cream to yellow ochre, with 4–7 fine brown spiral lines above periphery (including dark line at suture; sometimes increasing to 9 at end of last whorl); 7–12 brown oblique short stripes at periphery and suture, often faint or absent, occasionally continuing indistinctly across dorsal surface; base with 1–2 spiral brown lines at periphery, margin of umbilicus sometimes purplish brown; columella and parietal area purplish brown.

**Animal:** *Head-foot*: usually entirely unpigmented; sometimes slight blackish pigmentation behind head. *Penis* (Figures 84–87): filament slender, tapering, 30–40% total length; base thick, single large mamilliform penial gland (occupying 60–80% total length) with narrowly elongate reservoir; subepithelial glandular tissue at base of filament and around base of reservoir. *Pallial oviduct*: bursa not seen. *Egg capsule* (Figures 123, 127, 128): diameter 221.7  $\mu\text{m}$  (SD 13.1  $\mu\text{m}$ ,  $n=10$ ; ovum diameter 66.0  $\pm$  1.6  $\mu\text{m}$ ; Singapore; this study), of depressed cupola type with 3 concentric rings on upper side and pleated margin (like a thick cogwheel), containing single ovum. *Radula* (Figures 112, 113): all cusps sharply pointed, central cusp of rachidian tooth slightly apiculate; base of rachidian tooth with two sharp posterior denticles; outer marginal tooth with 3–4 pointed cusps, becoming smaller toward midline.

**Distribution:** *Habitat*: Among barnacles and oysters in upper eulittoral, on rocky shores and sea walls (Singapore).

*Range* (Figure 133): Singapore, Gulf of Thailand, northern Borneo.

*Records and material examined*: Singapore: Changi Point (BMNH; 1M, 4F, 3R); Changi South (BMNH; 4M, 2F); St. John's Island (BMNH; 2R, 1P). Thailand: Pattaya (Le Renard Colln). Sabah: Berhala Channel, Sandakan (USNM).

**Remarks:** The expansion rate of the shell is larger in this species than in other members of the genus, so that it achieves a slightly, but distinctly, patulous shape which is characteristic. The color pattern resembles that of *P. fasciata*, although the lines are usually less pronounced and the sutural and peripheral spots more developed. These two species are distinguished by their penial form,

the filament being slender and short in *P. patula*, and the mamilliform gland relatively larger. Their egg capsules differ in shape in samples of *P. patula* from Singapore and *P. fasciata* from Hong Kong. They have not yet been found syntopically, but their known ranges appear to overlap in northern Borneo; additional collecting in the region may well reveal wider sympatry. The radula of *P. patula* is peculiar, showing a pair of sharp posterior denticles on the base of the rachidian tooth (Figures 112, 113). Among other littorinids, similar denticles have been described only in *Melarthaphe neritoides* (Bandel, 1974: figs. 58, 59), but the structures are closer to the posterior edge of the tooth in *P. patula*, and are probably not homologous. Slight development of basal denticles has been found in one example of *P. fuscopiperata* and one of *P. isseli*. One specimen from the type locality showed both a fully formed pallial oviduct and a well developed penis (see remarks on pseudo-hermaphroditism under *P. habei*). This is the rarest of all the *Peasiella* species in museum collections, perhaps because of its limited geographical range; in Singapore it occurs abundantly.

*Peasiella fasciata* new species

(Figures 14–17, 49–51, 88–91, 106, 107, 117, 122, 125, 126, 134)

*Peasiella infracostata*.—Reid, 1989a:61–64, fig. 12, fig. 30 (radula), fig. 48 (penis), fig. 112 [in part, includes *P. infracostata*, *P. fuscopiperata*, *P. patula*, *P. habei*; not *P. infracostata* (Issel, 1869)]. Reid, 1992:194, fig. 1c (penis), fig. 2c (oviduct), pl. 1, figs. i, l, m [in part, includes *P. habei*].

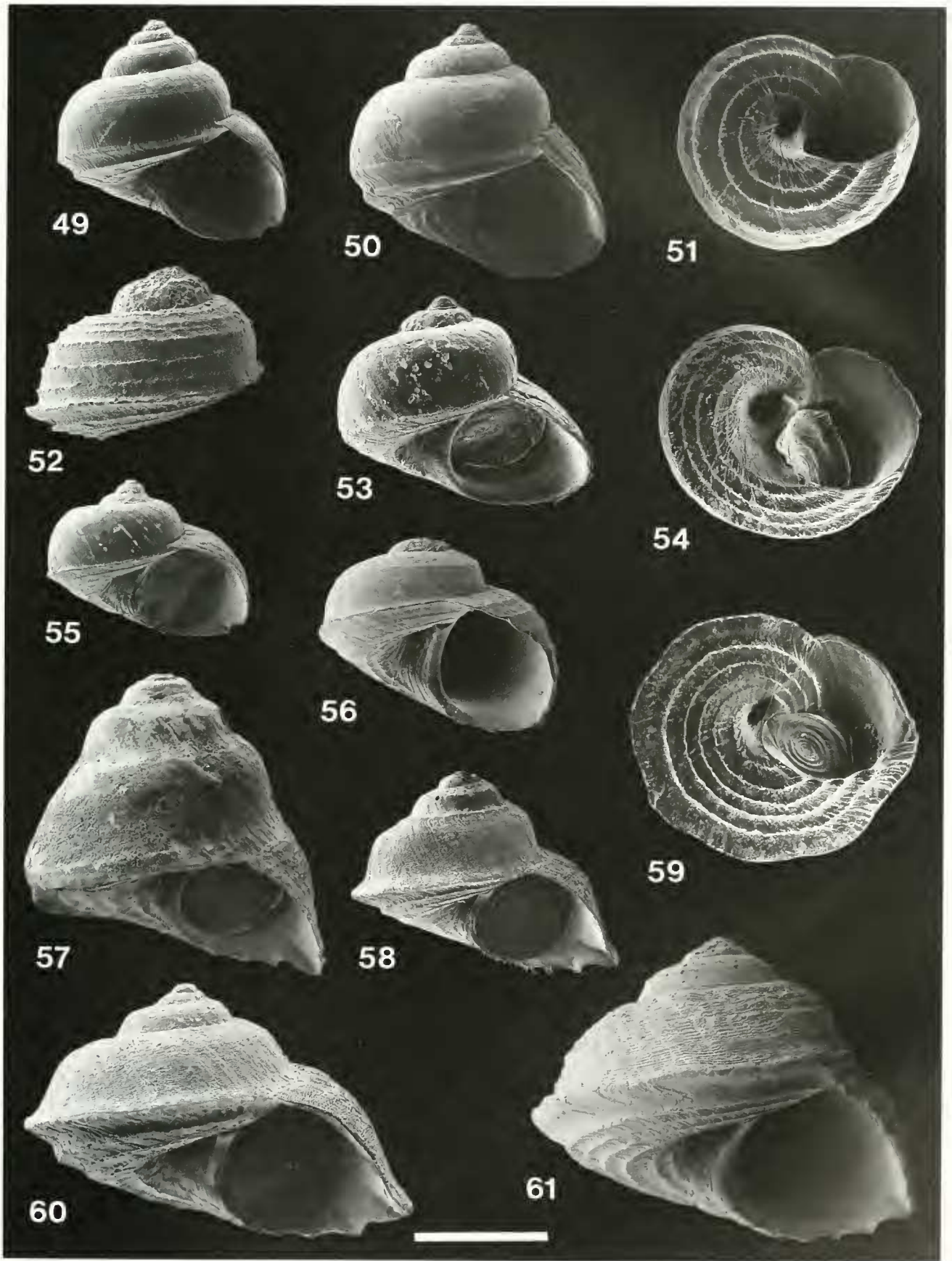
**Etymology:** Latin *fasciatus*, banded, in reference to color pattern.

**Types:** Holotype BMNH 1996272 (Figure 15); 5 paratypes BMNH 1996273; 1 paratype AMS C203254. Type locality: Turtle Bay, Cape Ferguson, Queensland, Australia.

**Shell** (Figures 14–17, 49–51, 106, 107): Adult size range 1.3–2.5 mm diameter. *Shape*: turbate to depressed turbate (H/D 0.78–1.12); outline domed; whorls well rounded, suture distinct; periphery uniformly rounded, or angled, or marked by a more or less prominent rib; base rounded; umbilicus small or almost closed; columella narrow, uniformly rounded. *Sculpture*: protoconch 240  $\mu\text{m}$  diameter, 2.6 whorls, protoconch I smooth, protoconch II with scattered small granules and narrow wavy or straight ridges, of which 6 are visible above suture (Figures 106, 107); teleoconch whorls

---

Figures 49–51. *Peasiella fasciata*, Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). 52–56. *Peasiella patula*. 52. Changi Point, Singapore (BMNH 1996278). 53–55. St. John's I., Singapore (BMNH 1996387). 56. Pataya, Thailand (LR 99012). 57–61. *Peasiella habei*. 57. 4–5 km SW Tsutsu, Tsushima I., Nagasaki Pref., Japan (BMNH 1996389). 58, 59. Nejiko, Hirado I., Nagasaki Pref., Japan. 60. Ma Liu Shi, Tolo Harbour, Hong Kong (BMNH 1996393). 61. Zampa Point, Okinawa, Japan (AMS C146702). Scale bar = 1 mm



smooth above periphery; with fine spiral microstriae, rarely with 3–4 faint grooves; 3–4 ribs on base (rarely 1–6), becoming stronger toward periphery. *Color*: translucent cream to opaque grayish white; pattern of brown, dark red-brown or black lines or bands, numbering 2–8 above periphery on last whorl (only 2–4 on spire whorls), bands often alternately thick and thin on last whorl; in addition sometimes 6–13 faint brownish spots at suture and periphery; 2–4 dark lines in grooves at periphery of base; base of columella and umbilical area sometimes dark purplish brown.

**Animal:** *Head-foot*: front of head blackish, with a separate black band across base of snout; tentacles unpigmented or with single longitudinal black line; foot unpigmented or with blackish sides. *Penis* (Figures 88–91): filament 40–50% total length, cylindrical and rounded at tip; base thicker, with single mamilliform penial gland of moderately large size (30–40% total length). *Pallial oviduct*: bursa present. *Egg capsule* (Figures 122, 125, 126): diameter 215.4  $\mu\text{m}$  (SD 5.8  $\mu\text{m}$ ,  $n=10$ ; ovum diameter  $77.8 \pm 2.9 \mu\text{m}$ ; Hong Kong; this study), of depressed cupola type with 4 concentric rings on upper side and pleated margin with peripheral keel, containing single ovum. *Radula* (Figure 117): cusps pointed, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 5–6 long, pointed cusps, outermost more rounded, becoming smaller toward midline.

**Distribution:** *Habitat*: among algae in rock pools (type locality; A. Mitchell); among short calcareous green algae and *Caulerpa*, on wave-exposed rocky platform (Cape Dampier; P. H. Colman); among eulittoral cobbles, crevices in granite and sedimentary rocks, among *Saccostraea*, on fairly sheltered and wave-exposed coasts (Hong Kong; J. D. Taylor, Y.-M. Mak). Appears to be generally scarce.

*Range* (Figure 134): Queensland, New Guinea, Borneo, Vietnam, Hong Kong, Taiwan.

*Records and material examined*: Queensland, Australia: Facing Island, Port Curtis (AMS); Turtle Bay, Cape Ferguson (AMS; 1M, 1R); Halfmoon Bay, Cairns (AMS); Green Island (AMS); Port Douglas (AMS). New Britain, Papua New Guinea: Uvol Mission, near Cape Dampier (AMS; 3M, 2F, 2P); Duke of York Island, Rabaul (AMS). Sabah: Bak-Bak, 9.6 km N Kudat (USNM). Vietnam: La Table Island, Tonkin (MNHN). Hong Kong: Wu Kwai Sha (BMNH; 2M, 2R); Peng Chau (BMNH; 1M); Hoi Ha (BMNH; 2F); Cape d'Agnilar (BMNH). Taiwan: Shi Cheng, Taipei (BMNH).

**Remarks:** The first evidence that this species was distinct from *P. habeii* (both confused under *P. infracostata* by Reid, 1989a, 1992) was provided by their differently shaped egg capsules in Hong Kong (Figures 122, 124). Differences in shell shape and penial form were then recognized, as described in the Remarks on *P. habeii*. The shell of *P. fasciata* is easily recognized by its combination of dark spiral lines, turbinate shape with well-

rounded whorls, and small umbilicus. Spiral color bands are found in some other *Peasiella* species, especially on the spire whorls, but are only well-developed on the last whorl in one other species, *P. patula*, which is distinguished by its patulous shape. Anatomically, *P. fasciata* is characterized by its penis with long, cylindrical filament and moderately large mamilliform gland. As in *P. infracostata* and *P. fuscopiperata*, the shell can be opaque and solid, or translucent, although it is never as delicate as in some examples of those species. This species is rare in collections.

*Peasiella habeii* new species

(Figures 18–24, 57–61, 92–98, 114–116, 124, 129, 130, 135)

*Littorina-capsula habeii* Tokioka, 1950:151–152, fig. 6.1 (egg capsule) [Ago and Tanabe Bays, Japan; name unavailable, see below]. Habe, 1956:117–121.

*Peasiella roepstorffiana*.—Habe, 1956:118–121, fig. A (egg capsule). Oyama & Takemura, 1961: *Peasiella* and *Littorinopsis* pl., figs. 1–3. Yamamoto & Habe, 1962:16, pl. 3, figs. 3, 4, figs. 34, 35 (egg capsule). Amio, 1963:303, figs. 22a, b (egg capsule). Habe, 1964:28, pl. 9, fig. 23. Higo, 1973: 46. Habe, 1984:11, fig. 1. Ohtsuka & Yoshioka, 1985:232, fig. 4B. Okutani, 1986:71, unnumbered pl. Fukuda, Mashino & Sugimura, 1992:57, pl. 43, fig. 126. Higo & Goto, 1993:74. [All not *P. roepstorffiana* (Nevill, 1885)].

*Peasiella infracostata*.—Reid, 1989a:61–64, fig. 10, fig. 29 (radula), fig. 47 (penis), fig. 64 (egg capsule), fig. 111 [in part: includes *P. infracostata*, *P. fuscopiperata*, *P. patula*, *P. fasciata*]. Choe, 1992:290, 591, fig. 56. Reid, 1992:194, pl. 1f [in part: includes *P. fasciata*]. Choe & Park, 1993: 19–20, text fig. 2. [All not *P. infracostata* (Issel, 1869)].

**Etymology:** To honor Prof. T. Habe, who has contributed much to the study of Japanese littorinids.

**Types:** Holotype BMNH 1996274 (Figure 20); 9 paratypes in alcohol BMNH 1996275. Type locality: Esu Cape, Shirahama, Wakayama Prefecture, Japan.

**Nomenclature:** Uniquely for a littorinid, the first name for this species was applied to its egg capsules. Tokioka (1950) described two types of littorinid egg capsules in plankton hauls from Ago and Tanabe Bays in southeastern Honshu, to which he gave Latin names. Since the littorinids that produced the capsules were not known, he coined a new genus *Littorina-capsula*. Subsequently, Habe (1956) showed that one of these capsules, *Littorina-capsula habeii*, was the egg of the common Japanese species of *Peasiella* (which he misidentified as *P. roepstorffiana*). However, it is debatable whether the specific name given by Tokioka is nomenclaturally available. Habe (1956) apparently considered it so, printing it in italics. Others have not done this, and thus appear to have judged it unavailable (Amio, 1963; Reid, 1989a). In its favour, it can be argued that the name is unambiguous, since the egg capsule is distinctly different from those of other known Japanese littorinids. A name based on only one stage in a life cycle, while undesirable, is not thereby made unavailable (ICZN Art.

17). The generic name *Littorina-capsula* is unavailable (since it is not accompanied by fixation of a type species, ICZN Art. 13b), but this does not affect the standing of a specific name combined with it (ICZN Art. 11h). The inclusion of a hyphen in the generic name is an incorrect spelling (ICZN Art. 32c), and does not indicate that the name is non-binominal. On the other hand, it appears that Tokioka did not intend to introduce new names for littorinid species, for he stated: 'For convenience of recording these capsules met with during our plankton studies, I propose to give them the following provisional names'. This, we believe, debar the names from nomenclatural consideration, since the ICZN Code specifically excludes names proposed 'as means of temporary reference and not for formal taxonomic use as scientific names' (ICZN Art. 1b). This case is a complex and unusual one, and is open to alternative interpretations. If Tokioka's name were to be accepted, the egg capsules studied by him would have the status of type material; inquiries from the Seto Marine Laboratory have shown that no such material exists there (S. Yamato, pers. comm.). In this case, our choice is to re-describe the species as new, based on type material of adult animals collected near the locality of Tokioka's capsules. However, in recognition of Tokioka's discovery of the egg capsules, his intention to honor Prof. T. Habe, and to provide continuity, we use the same specific name.

In the Japanese literature this species has generally been misidentified as *P. roepstorffiana*, while Reid (1989a, 1992) incorrectly included it under *P. infracostata*.

**Shell (Figures 18–24, 57–61):** Adult size range 1.6–3.8 mm diameter. *Shape:* equilaterally conical or slightly more depressed (H/D 0.60–1.03); outline domed; whorls almost flat-sided or rounded or slightly shouldered, suture inconspicuous or impressed; peripheral keel prominent, often a projecting flange, rarely slightly undulating; base flat to slightly rounded; umbilicus usually narrow; columella narrow, curved at base. *Sculpture:* protoconch 230 µm diameter, 2.5 whorls, sculpture not preserved, apex usually eroded; teleoconch whorls usually smooth, with spiral microstriae, sometimes with 6–11 equidistant spiral grooves above periphery in largest specimens; 3–5 (rarely 6) sharp ribs on base, equidistant or becoming closer around umbilicus; basal ribs (and occasionally dorsal ribs) may bear periostracal bristles. *Color:* variable; fawn, cream or ochre, paler at periphery, with oblique (sometimes axial or zigzag) anastomosing brown stripes (sometimes faint, especially in Hong Kong), always darkening to form single row of 7–12 more or less conspicuous large brown or black spots near periphery (occasionally fusing to give a solid spiral band) which become narrower as they extend over pale peripheral keel; pattern on spire whorls darker, often blackish where eroded (especially in Japan); occasionally 2–4 spiral brown lines on spire whorls (common in Okinawa), usually disappearing on last whorl, but rarely persisting as 5–9 spiral lines; base ochre to brown, darker

near umbilicus and in peripheral groove adjacent to keel; sometimes shell more darkly patterned, spire and base black, last whorl with oblique anastomosing black stripes on whitish ground (some from Japan and northern China).

**Animal:** *Head-foot:* front of head blackish, with separate black band across base of snout, occasionally almost unpigmented; tentacles unpigmented; sides of foot sometimes slightly pigmented. *Penis (Figures 92–98):* filament long (50–60% total length), vermiform; base slightly thicker, 1 (rarely 0 or 2) small mamilliform penial gland. *Pallial oviduct:* bursa present. *Egg capsule (Figures 124, 129, 130):* diameter 261.3 µm (SD 0.5 µm, n=10; ovum diameter 68.3±2.3 µm; Hong Kong; this study), 150–250 µm (Japan; Tokioka, 1950; Amio, 1963; Ohtsuka & Yoshioka, 1985), of cupola type with 4 concentric rings on upperside, containing single ovum. *Radula (Figures 114–116):* cusps pointed, central cusp of rachidian tooth slightly apiculate, major cusp of lateral and inner marginal teeth sometimes slightly rounded; outer marginal tooth with 4–6 (rarely 3) long, pointed cusps, outermost more rounded, becoming smaller toward midline.

**Distribution:** *Habitat:* In Japan this species is abundant in crevices and among barnacles in the middle and upper eulittoral zone, on sheltered and moderately exposed rocky shores; on exposed shores it shows a preference for surfaces protected from wave action (Mori *et al.*, 1985a, b; Tanaka *et al.*, 1985). In Hong Kong and Taiwan it appears to be rare, and is found among barnacles and oysters in the uppermost eulittoral zone on sheltered shores.

*Range (Figure 135):* China, Korea, Taiwan, Ryukyu Islands, Japan.

*Records and material examined:* China: Ma Liu Shu, Tolo Harbour, Hong Kong (BMNH; IM, 1F, 2R); Lok Wo Sha Bay, Tolo Channel, Hong Kong (BMNH); Pao-tai, Xiamen (BMNH; IM, 1F); Gu Leng Yu, Xiamen (BMNH; 1M, 3F, 1R, 1P); Tai Ping Bay, Qingdao (BMNH; 2M, 2F, 1R); Hui Quan Bay, Qingdao (BMNH). Korea: Taesori, Sangch'uja I. (Choe, 1992; Choe & Park, 1993). Taiwan: Yehliu, Taipei (BMNH). Japan: 1.5 km WNW Onna, Okinawa (AMS); Bolo Point, Okinawa (AMS, 1F, 1R; USNM, NSMT); Baten, Okinawa (BMNH; 1M, 2F, 3R); Tomioka, Kumamoto Pref. (NSMT, 2R); Nagasaki (USNM); Omura Bay, Nagasaki Pref. (NSMT); Goto, Nagasaki Pref. (AMS); Nejiko, Hirado I., Nagasaki Pref. (BMNH; 1M, 1F); Tsutsu, Tsushima I., Nagasaki Pref. (BMNH); Fukuyoshi, Fukuoka Pref. (KU); Kure, Hiroshima Pref. (KU); Hanazura, Kochi Pref. (MNH); Tatsukushi, Kochi Pref. (USNM, NSMT); Shirahama, Tanabe Bay, Wakayama Pref. (BMNH; 5M, 2F, 1R; USNM, NSMT); Shionomisaki, Wakayama Pref. (NSMT); Kuchino, Shiznoka Pref. (BMNH, 4M, 2R); Arasaki, Kanagawa Pref. (USNM, NSMT); Oga Peninsula, Akita Pref. (KU); Asamushi, Ao-

mori Pref. (USNM, NSMT); 2.5 km N Tomari, Aomori Pref. (AMS); Kominato, Aomori Pref. (LACM).

**Remarks:** This species is variable in conspicuous features of the shell including color, spire profile and sculpture, but consistent characteristics are the row of dark spots above the periphery, which extend onto the pale peripheral keel, the darker and often black spire whorls, and the prominent keel at the periphery. There are some recognizable geographical trends in shell characters. In Japan and northern China the shape is taller, with flatter whorls and a sharper peripheral keel; periostracal bristles are present at least on the base of most well-preserved specimens; the spire, usually eroded, is black or darkly patterned (Figures 18–21, 57–59). Shells from the southern parts of the range are distinctly different. Those from Okinawa have a pale pattern; the dark peripheral spots are most conspicuous on the spire whorls, which are also often marked by 2–4 spiral brown lines; the whorls are sometimes rounded at the shoulder, and usually bear strong spiral grooves above the periphery, and the peripheral keel is less pronounced; periostracal bristles have not been seen (Figures 23, 61). Shells from Hong Kong and southern China are similar in shape to those from Okinawa, but are usually smooth above the periphery, sometimes bear periostracal bristles on the base, and the color is ochre with strong peripheral spots and darkly patterned spire (Figures 24, 60). However, these southern populations are also variable, and intermediates apparently connect them with the typical northern forms (Figure 22). Additional material, particularly from the Ryukyu Islands, would be desirable to investigate this variation in more detail, and to confirm our interpretation. The penial shape is similar throughout the range. The egg capsules from Hong Kong (figures 124, 129, 130) are almost identical in shape to those figured from Japan by Tokioka (1950; reproduced by Yamamoto & Habe, 1962; Reid, 1989a), Habe (1956) and Ohtsuka & Yoshioka (1985). However, at a diameter of 261  $\mu\text{m}$  they are slightly larger in size than Japanese capsules, measured as 150–200  $\mu\text{m}$  (Tokioka, 1950), 150  $\mu\text{m}$  (Amio, 1963) and 220–250  $\mu\text{m}$  (Ohtsuka & Yoshioka, 1985).

The rounded shells with lined pattern on the spire that can be found in Okinawa bear some similarity to those of *P. fasciata* from Hong Kong. This led Reid (1989a) to consider them conspecific (as *P. infracostata*). However, new material from Hong Kong has shown that both species occur there, although so far they have not been collected syntopically (i.e. on the same shores). In Hong Kong the shells of *P. habei* only occasionally bear 1–2 indistinct spiral brown lines above the periphery on

the last whorl, and their conspicuous peripheral spots and darkly patterned spire differ from the 4–8 strong spiral lines of local examples of *P. fasciata*. Anatomically, the mamilliform penial gland of *P. habei* is smaller and the penial filament relatively narrower and slightly more elongate than in *P. fasciata*. The egg capsules of these two species (sampled in Hong Kong) also differ (Figures 122, 124).

Two other species are sometimes sympatric with *P. habei* in the southern part of its range and might be confused with it, *P. lutulenta* in Hong Kong and *P. roepstorffiana* in the southern Ryukyu Islands, Taiwan and Hong Kong. *Peasiella lutulenta* has 5–9 strong spiral ribs above the periphery, usually a gap between inner and outer series of ribs on the base (ribs all equidistant in *P. habei*), the columella has a thickened angulation at the base, and the color pattern is of 7–13 broad and irregular, dark axial stripes (see Reid, 1989a, 1992). Anatomically the two are closely similar; the penial filament of *P. habei* is slightly narrower and more elongate, and there are 4–6 cusps on the outer marginal tooth, but only 3 in *P. lutulenta*. *Peasiella roepstorffiana* (Figures 142–145) has 4–13 strong spiral grooves above the periphery, frequently shows radial plications near the suture and periphery, which give rise to strong crenulations of the peripheral keel; the innermost one third of the basal radius lacks ribs; the color is often bright chrome yellow or orange, with peripheral brown spots or band. Anatomically, *P. roepstorffiana* from Hong Kong lacks the mamilliform penial gland, and the copulatory bursa is absent.

Some abnormalities of the reproductive tract of *P. habei* have been found. A single specimen from Shiznoka Prefecture had no mamilliform penial gland (Figure 98), and one (parasitized by trematodes) from Tanabe Bay had two glands of normal size (Figure 97); in each case normal specimens occurred in the same lots. One other specimen from the latter sample had both a small, fully formed penis and a small oviduct. Genuine hermaphroditism has been described in only one littorinid genus, *Mainuaringia* (Reid, 1986b), but pseudo-hermaphroditism (involving development of a penis and other male characters in females) is known in several littorinid genera (Reid, 1986b, 1996), and is sometimes a response to pollution by organotin compounds (Bauer *et al.*, 1995). *Peasiella* species are not known to be truly hermaphroditic, and this example is probably a case of pseudo-hermaphroditism.

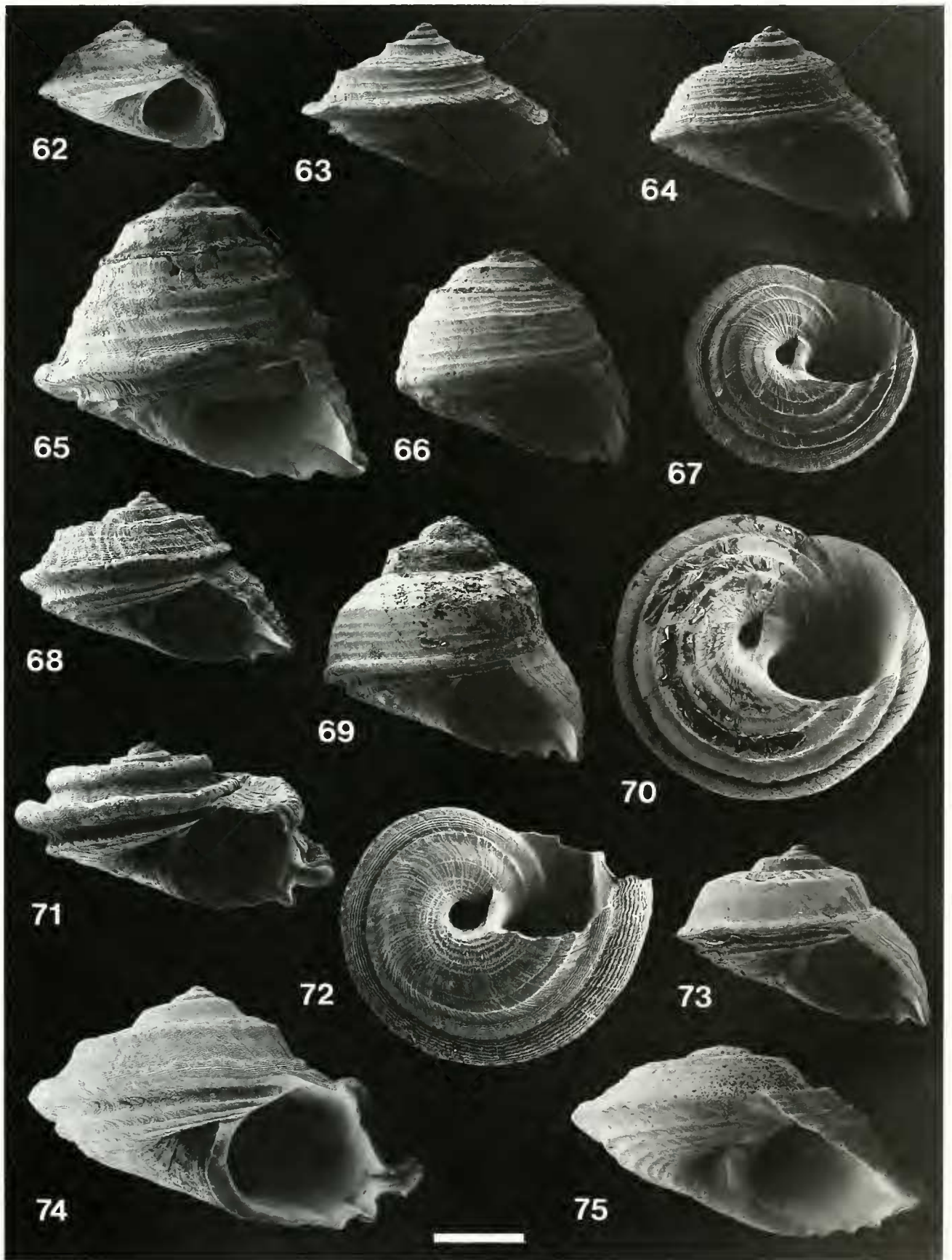
*Peasiella isseli* (Semper in Issel, 1869)  
(Figures 25–29, 62–67, 99–101, 118, 119, 136)

*Trochus* sp. Andouin, 1826:42

*Risella isseli* Semper in Issel, 1869:194, 347 [refers to Savigny,

→

**Figures 62–67.** *Peasiella isseli* 62. Lectotype of *Risella isseli* Semper in Issel, 1869, Red Sea (MNHN). 63, 65, 66. Suez, Egypt (BMNH 1888.10.14) 64, 67. Hurghada, Egypt (BMNH 1996395). 68–75. *Peasiella mauritiana*. 68. Tiwi Beach, 30 km S Mombasa, Kenya. 69, 70, 73. Sedhi, Al Khaysah, Oman 71. Kuwait. 72, 74. Bandar Khayran, Oman. 75. Baie Ternay, Mahé, Seychelles. Scale bar = 1 mm.



1817: pl. 5, figs. 35.1, 35.2; lectotype (Reid, 1989a; fig. 62) + 2 paralectotypes MNHN, seen; Suez (Reid, 1989a); 2 paralectotypes in MGD ex-Semper Colln, seen, from Zanzibar are *P. mauritiana*. Pallary, 1926:84, pl. 5, fig. 35.1, 35.2. Lamy, 1938:71. Moazzo, 1939:183. Bouchet & Danrigal, 1982:13, fig. 65.

*Risella (Peasiella) isseli*.—Nevill, 1885:160–161 [in part; includes *P. mauritiana*]. Tryon, 1887:263, pl. 50, figs. 39, 40.

*Peasiella isseli*.—Franc, 1956:25. Mastaller, 1979:40. Reid, 1989a:60–61, fig. 13, fig. 50 (penis), fig. 56 (sperm), figs. 97, 98, 101, 103 [in part, includes *P. mauritiana*].

*Trochus sismondae* Issel, 1869:225–226, pl. 2, fig. 13 [holotype MGD, seen; Suez].

*Risella isseli* var. *carinata* Pallary, 1926:84–85, pl. 5, fig. 36 [reproduced from Savigny, 1817; syntype MNHN, seen; Suez].

*Risella isseli* var. *undata* Pallary, 1926:84, pl. 5, fig. 35.3 [reproduced from Savigny, 1817; types not in MNHN; Suez].

**Nomenclature:** Throughout its taxonomic history this species, endemic to the Red Sea, has been confused with *P. mauritiana*, and the two taxa have not previously been distinguished at the specific level. In the original description, Issel referred to the figures of Savigny (1817) based on Egyptian specimens. He also mentioned his own material from Suez and Semper's from Zanzibar, of which the latter (in MGD) is *P. mauritiana*. Reid (1989a) designated one of the shells from the Savigny Collection as the lectotype, and restricted the type locality to Suez, thereby fixing the identity of this species.

**Shell (Figures 25–29, 62–67):** Adult size range 1.7–4.2 mm diameter. *Shape:* conical to depressed conical (H/D 0.55–1.23); outline domed; whorls usually with rounded or angled shoulder, occasionally flat or only gently rounded; suture usually distinct; periphery sharply angled, with prominent rib or flange; dorsal sculpture sometimes slightly rugose, but only rarely does peripheral flange show slight crenulation; base flat or slightly rounded; umbilicus small to moderate; columella rounded, sometimes with a slightly thickened angle at base. *Sculpture:* protoconch 240  $\mu$ m diameter, 2.3 whorls, protoconch II with scattered small granules and narrow wavy or straight ridges, of which 5 are visible above suture (as in Figures 106, 107, of *P. fasciata*); teleoconch whorls with 6–15 narrow ribs, uniform or unequal in size, above periphery; rib at shoulder sometimes slightly enlarged; surface above periphery covered with fine spi-

ral microstriae; base with 4–6 (rarely 2–7) ribs, larger toward periphery. *Color:* extremely variable; uniform cream, ochre, orange-brown, dark chestnut brown or entirely black; often with darker pattern of fine dots or lines in dorsal grooves; dorsal surface sometimes with fine white and brown marbled pattern; rarely a dark spiral band on dorsal surface; sometimes 7–15 brown spots on white peripheral keel; rarely pale sutural spots in addition to darker peripheral spots, but only very seldom does an indistinct pattern of broad radial bands appear; spire sometimes pink or crimson; apex often lilac or blackish; base lacking color pattern or with small spots in grooves.

**Animal:** *Head-foot:* head unpigmented or blackish in front, separate black band across base of snout; tentacles usually with 2 longitudinal black lines; sides of foot with some black pigmentation or unpigmented. *Penis (Figures 99–101):* filament long (50% total length), tapering at tip; base thicker, with single mamilliform penial gland of moderate size. *Pallial oviduct:* large anterior bursa present. *Radula (Figures 118, 119):* cusps pointed, major cusp of lateral and inner marginal teeth slightly rounded, central cusp of rachidian tooth sometimes slightly apiculate; base of rachidian tooth occasionally with slight development of pair of posterior denticles; outer marginal tooth with 4 pointed cusps, outermost more rounded, becoming smaller toward midline.

**Distribution:** *Habitat:* Abundant under coral blocks in upper eulittoral on a moderately sheltered shore (Egypt; D. G. Reid).

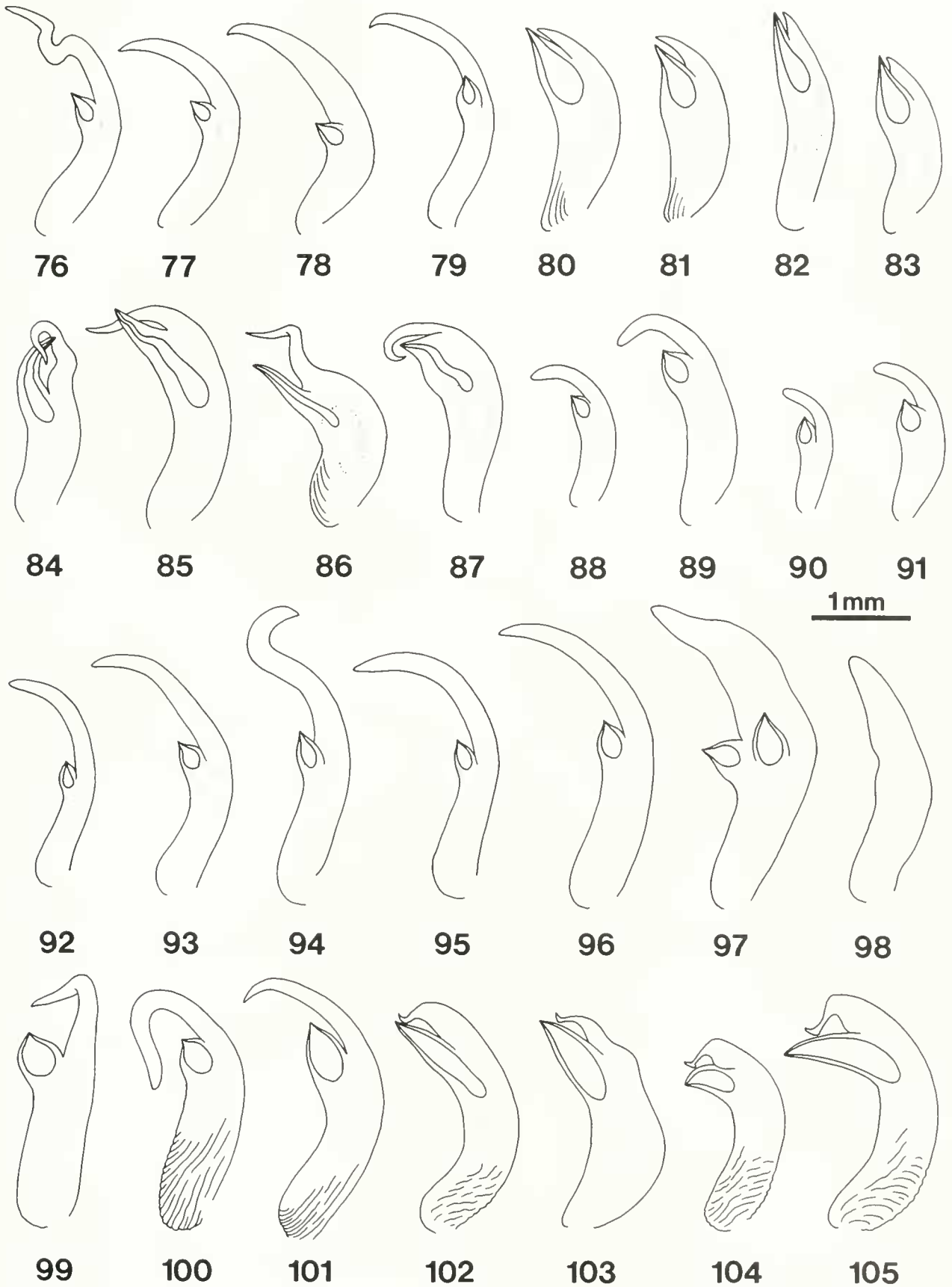
*Range (Figure 136):* Red Sea and Aden.

*Records and material examined:* Israel: Eilat (BMNH, 1M, 2F; USNM, ANSP). Egypt: Faraun Island, Gulf of Aqaba (IID); Ras el Kura, Dahab, Sinai (HD); Suez (BMNH, 1P, 2R; MNHN); Suez Canal (Tillier & Bavay, 1906; Moazzo, 1939); Hurgada (BMNH, 3M, 2F, 2R; IID). Sudan: Dungunab Bay (BMNH); Port Sudan (BMNH; ANSP). Saudi Arabia: Jeddah (USNM, MNHN). Eritrea: Massawa (BMNH, NM); Dahlak Archipelago (BMNH). Yemen: Périm Island (MNHN); Aden (MNHN).

**Remarks:** The shells of *P. isseli* and *P. mauritiana* are very similar, and the two have not previously been dis-

→

**Figures 76–79.** Penes of *Peasiella infracostata*. **76, 77.** Tiwi Beach, 30 km S Mombasa, Kenya. **78.** Karachi, Pakistan. **79.** Ras al-Hadd, Oman. **80–83.** Penes of *Peasiella fuscopiperata*. **80, 81.** Tiwi Beach, 30 km S Mombasa, Kenya. **82, 83.** Mapelane, Zululand, South Africa (NM D5822). **84–87.** Penes of *Peasiella patula*. **84–86.** Changi South, Singapore. **87.** Paratype, Changi Point, Singapore (BMNH 1996278). **88–91.** Penes of *Peasiella fasciata*. **88, 89.** Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). **90.** Wu Kwai Sha, Hong Kong. **91.** Peng Chau, Hong Kong. **92–98.** Penes of *Peasiella lapei*. **92.** Tai Ping Bay, Qingdao, China. **93.** Shirahama, Wakayama Pref., Japan. **94.** Baten, Okinawa, Japan. **95–97.** Fujishima, Tanabe Bay, Wakayama Pref., Japan. **98.** Kuchino, Suruga Bay, Shizuoka Pref., Japan. **99–101.** Penes of *Peasiella isseli*, Hurgada, Egypt. **102–105.** Penes of *Peasiella mauritiana*. **102.** Khor Uajar, Ras al-Hadd, Oman. **103.** Anse La Mouche, Mahé, Seychelles. **104.** Merawwah L., Abu Dhabi. **105.** Tiwi Beach, 30 km S Mombasa, Kenya. Note that structure of mamilliform penial glands is visible by transparency; mucous reservoir is shown by solid line, and extent of subepithelial glandular tissue by dotted line. The penial base is sometimes wrinkled.





tinguished as separate species. From the new anatomical material available for each species, it is clear that they can be diagnosed by the form of the penis. This is of the common type for the genus in *P. isseli*, with long filament and small mamilliform gland, whereas in *P. mauritiana* from throughout its large range it has a short filament with mucronate and hooked tip, and a large gland. Having separated the two using this character, correlated differences in shell shape and coloration can be recognized. In both, the development of the shoulder angulation is variable; in *P. isseli* it is often absent or represented only by an angulation of the profile, more rarely by a prominent rib; in *P. mauritiana* the shoulder is usually marked by a sharp angulation, often with an enlarged or even carinate rib. The coloration is also different; in *P. mauritiana* there is usually a pattern of obliquely radial lines or stripes, often darker at the suture and periphery; in *P. isseli* the color is highly variable, but radial stripes rarely appear, and the apex is often pink or blackish. Using these characters, together with knowledge of the regional variation in the shell of *P. mauritiana*, it has been possible to identify shells with confidence. So far, it appears that *P. isseli* is restricted to the Red Sea and Aden, whereas *P. mauritiana* is widespread in the Indian Ocean and Persian Gulf. The two apparently occur sympatrically just at the mouth of the Red Sea. Two dead shells of *P. isseli* have been recorded from Aden (MNHN), from which locality five other samples contained only *P. mauritiana*. Both have been found together in a single lot of dead shells from Périm Island, South Yemen (Jousseume Colla, MNHN), which contained 50 *P. isseli* and 8 *P. mauritiana*, readily separated by their shell characters.

The only other species to occur sympatrically with *P. isseli* is *P. infracostata*. These two are readily distinguished by the presence of spiral ribs above the periphery in *P. isseli* (absent in *P. infracostata*), and by the color pattern of oblique or zigzag lines in *P. infracostata*. The shape of the penis is, however, similar in both.

Most *Peasiella* species show variation in color pattern, sometimes on a regional or interpopulational scale. This species is unique in the genus in its extreme intrapopulational variation; shells from beneath the same rock may range from cream to patterned to black. Furthermore, occasional specimens can be found in which the color changes from cream on the spire to entirely black on the last whorl (Figure 26).

*Pcasiella mauritiana* (Viader, 1951)  
(Figures 30–34, 68–75, 102–105, 120, 121, 137)

*Risella isseli*.—Issel, 1869:194 [in part; includes *P. isseli*].

*Risella (Peasiella) isseli*.—Nevill, 1885:160–161 [in part; includes *P. isseli*]. Melville & Standen, 1901:364 [not Semper in Issel, 1869].

*Peasiella isseli*.—Reid, 1989a:60–61, figs. 14, 15, fig. 28 (radula), fig. 49 (head), fig. 97, 99, 100, 102, 104, 105 [in part; includes *P. isseli*]. Bosch *et al.*, 1995:46, fig. 119 [not *P. isseli* (Semper in Issel, 1869)].

*Risella infracostata*.—Dantzenberg, 1929:496 [not Issel, 1869].

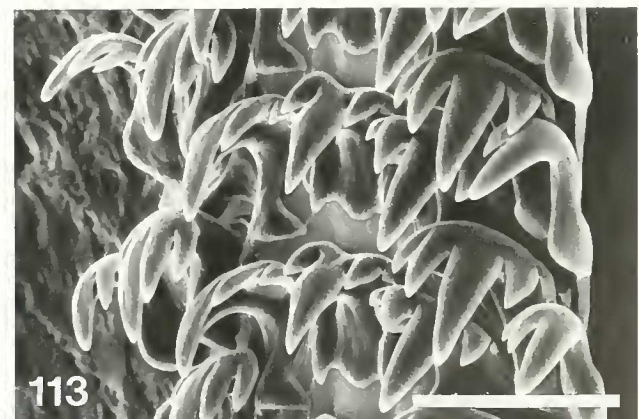
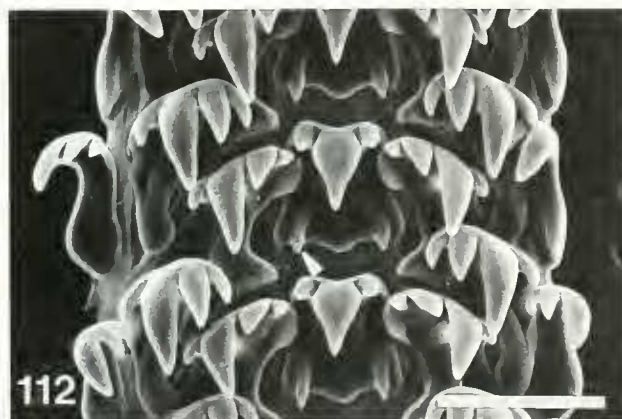
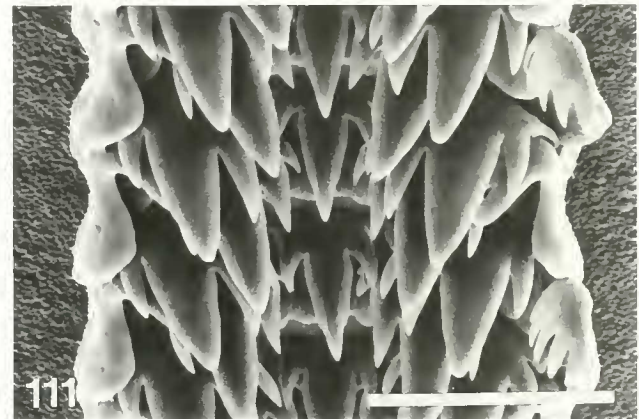
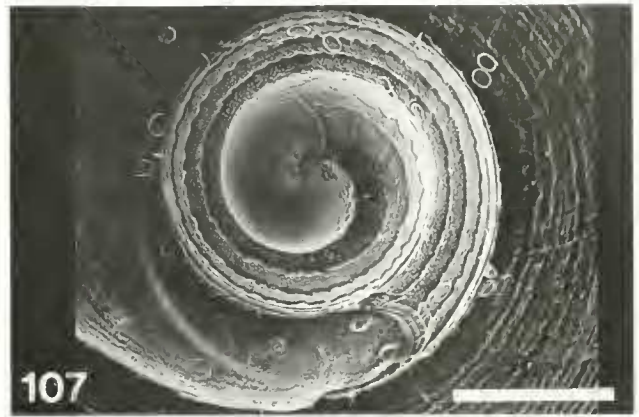
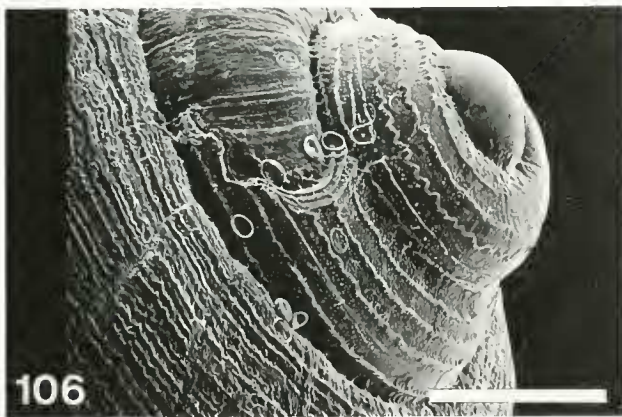
*Risella isseli* var. *mauritiana* Viader, 1951:149, pl. 3, figs 10, 11 [lectotype, here designated, Figure 30, + 2 paralectotypes, seen, BMNH 1989004; Grand Bay, Mauritius; 2 probable paralectotypes Mauritius Institute, not seen].

**Nomenclature:** Hitherto, this species has always been confused with *P. isseli*. It was first named, as a variety of that species, by Viader (1951). Two specimens of *Risella isseli* var. *mauritiana* were exhibited in the natural history museum of the Mauritius Institute (R. Gajeelee, pers. comm. 1985); these have not been examined, but are likely to have been syntypes. In addition, there are 3 specimens in the Winckworth Collection in BMNH, labeled '*Peasiella isseli* v. *mauritiana* Viader MS' in Winckworth's hand; these are from Grand Bay, one of the two localities mentioned in Viader's (1951) description. It is known that Winckworth received specimens from Viader (see also acknowledgement of Winckworth's assistance in determinations, Viader, 1951:136), and it is likely that this material was sent by Viader before Winckworth's death in 1950. Since Viader (1951) did not designate type specimens, a lectotype is here designated from the BMNH material (ICZN art. 74; recommendation 72B).

**Shell (Figures 30–34, 68–75):** Adult size range 1.6–5.6 mm diameter. **Shape:** highly variable; depressed conical to flattened (H/D 0.42–1.03); outline domed, straight or spire slightly concave; shoulder usually sharply angled, or with projecting rounded carina (some Persian Gulf and northern Oman specimens), or sometimes becoming rounded or even flattened on last whorl; suture usually distinct; periphery sharply keeled or flanged, or with flaring rounded carina (some Persian Gulf and northern Oman specimens); shoulder occasionally regularly rugose and peripheral flange with 7–8 slight crenulations (some East African specimens); base flat to rounded; umbilicus small to large; columella rounded, sometimes indistinctly thickened and angled at base.

→

**Figures 106, 107.** Protoconch of *Peasiella fasciata*, Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). **Figures 108, 109.** Radulae of *Peasiella infracostata*. **108.** Karachi, Pakistan (flat view, shell D=1.5 mm). **109.** Ras al-Hadd, Oman (flat view, shell D=1.9 mm). **110, 111.** Two views (flat and at 45°) of radula of *Peasiella fuscopiperata*, Tiwi Beach, 30 km S Mombasa, Kenya (shell D=1.7 mm). **112, 113.** Two views (flat and at 45° from side) of radula of paratype of *Peasiella patula*, Changi Point, Singapore (BMNH 1996278, shell D=1.7 mm); note posterior denticles on base of rachidian tooth (arrow). Scale bars: **106, 107** = 100 µm, **108–113** = 20 µm.



*Sculpture*: protoconch 220  $\mu\text{m}$  diameter, 2.2 whorls, protoconch II with scattered small granules and narrow wavy or straight ridges, of which 6 are visible above suture (as in Figures 106, 107, of *P. fasciata*); teleoconch whorls usually with 6–12 fine spiral ribs above periphery, sometimes only single rib at shoulder, or absent; surface above periphery covered with fine spiral microstriae; base with 4–7 (rarely 1–3) ribs, becoming weaker and more closely spaced around umbilicus; periostracum thicker than in other species of the genus, and may flake off from dry shells; ribs on base and rarely on dorsal surface may bear periostracal bristles (some Persian Gulf and northern Oman specimens). *Color*: cream to ochre; usually with dark brown oblique (opisthocline) lines or narrow stripes, numbering 6–11, often darkest or broadest at suture and periphery; in northern Oman and Persian Gulf oblique lines may number up to 23 on last whorl, anastomosing to produce 8–15 spots at suture and periphery; diagonal stripes occasionally present only at suture and periphery (some East African specimens); diagonal pattern only rarely entirely absent or developed only on spire (most specimens from Seychelles); often a single brown spiral line on early spire whorls; base unpatterned or with small brown spots on ribs, occasionally forming radial lines; parietal callus, columella base and umbilical margin sometimes brownish.

**Animal:** *Head-foot*: front of head blackish or with narrow black band only, separate black band across base of snout; tentacles with 2 longitudinal black lines; sides of foot with some black pigmentation or unpigmented. *Penis* (Figures 102–105): filament short (20–30% total length), with elongate, mucronate tip, distinctly hooked or minutely hammer-shaped at very tip; base thicker, finely wrinkled, with single large mamilliform penial gland (rarely absent) with elongate reservoir. *Pallial oviduct*: bursa present, apparently at posterior end of straight section. *Radula* (Figures 121, 122): cusps pointed, major cusp of lateral and inner marginal teeth slightly rounded, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 4 pointed cusps, outermost more rounded, becoming smaller toward midline.

**Distribution:** *Habitat*: intertidal rocks, pools and *Thalassodendron* flats in a sheltered bay (Inhaca Island; R. N. Killburn); barnacle zone on beach rock (Aldabra; J. D. Taylor); among barnacles in high eulittoral, on surf beach (Masirah Island; J. D. Taylor); crevices in limestone, in upper eulittoral, on sheltered coast and in tidal lagoon (Ras al-Hadd; E. Glover); among barnacles on

mangrove pneumatophores (Abu Dhabi; D. George); among *Crassostrea* (Kuwait; D. Jones).

*Range* (Figure 137): Zululand to Persian Gulf, Mauritius, Madagascar, Seychelles; excluding Red Sea.

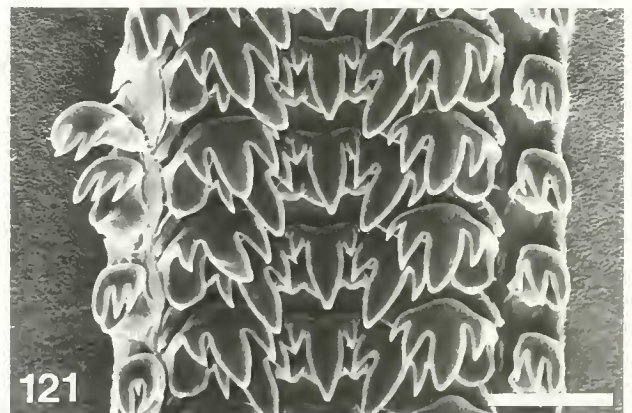
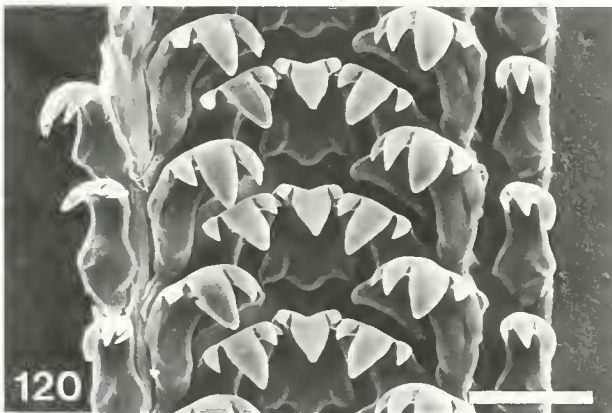
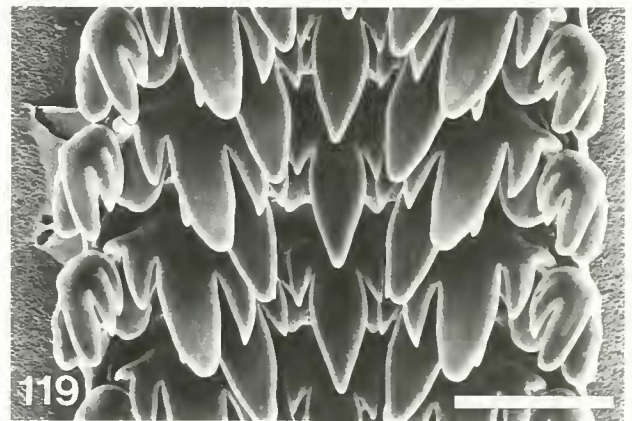
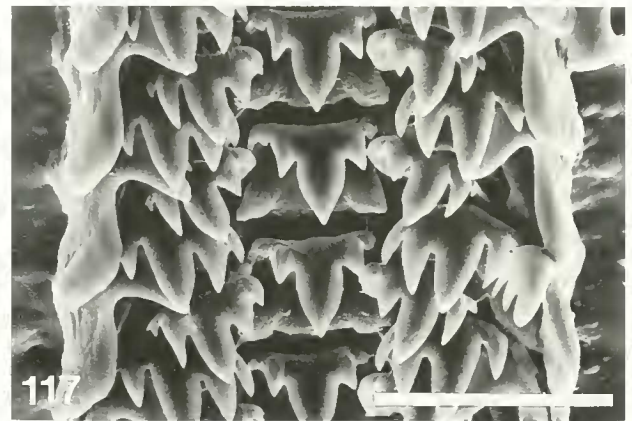
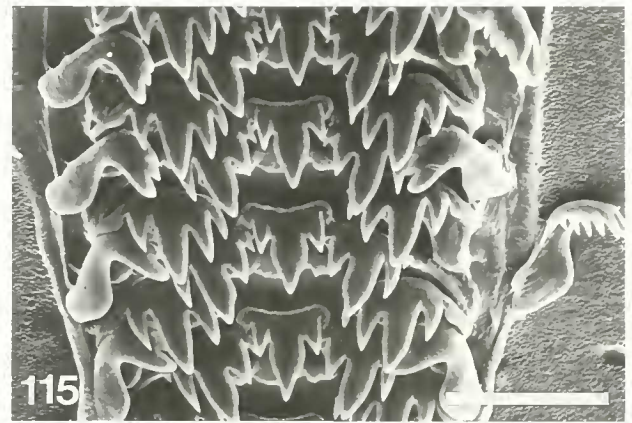
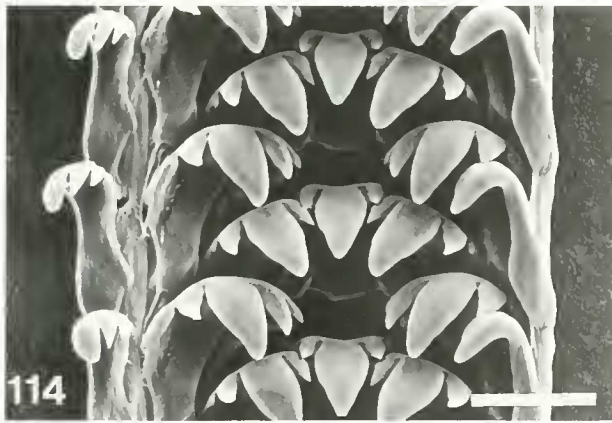
*Records and material examined*: South Africa: Mission Rocks, Zululand (NM). Moçambique: Inhaca Island (NM, 1M); Benguera Island (NM); Moçambique Island (NM). Tanzania: Zanzibar (BMNH). Kenya: Tiwi Beach, 30km S Mombasa (BMNH, 2M, 2F). Madagascar: Tuléar (MNHN); Mahajanga (IRSNB); Nossi-Bé (USNM, ANSP, MNHN, ZMA); Diego-Suarez (IRSNB). Île Mayotte (MNHN, 1M). Mauritius: Grand Bay (BMNH, NM); Pointe Radeau, S of Roches Noires (NM); Pointe d'Azur (NM). Seychelles: Aldabra (BMNH); Baie Ternay, Mahé (BMNH, 2R); Anse la Mouche, Mahé (BMNH, 1M, 1F; USNM); Northwest Bay, Mahé (ANSP). Djibouti (MNHN). Yemen: Périm Island (MNHN); Little Aden (BMNH, 2F); Aden (BMNH, MNHN). Oman: Hamran, Zufar (BMNH); Sudh (BMNH); Sadh (BMNH); Kuria Muria Islands (ZMA); Masirah Island (BMNH, 1F; ZMA, 2F); Sedh, Al Khaysah (BMNH); Khor Hajar, Ras al-Hadd (BMNH, 1M, 2F, 1R); Bandar Khayran (BMNH); Al Bustán, 3.2 km E Muscat (ZMA); Muscat (NM); N of Sharm (BMNH). Abu Dhabi: Merawah Island (BMNH, 3M, 1F). Qatar: Khor, Doha (BMNH). Kuwait (BMNH).

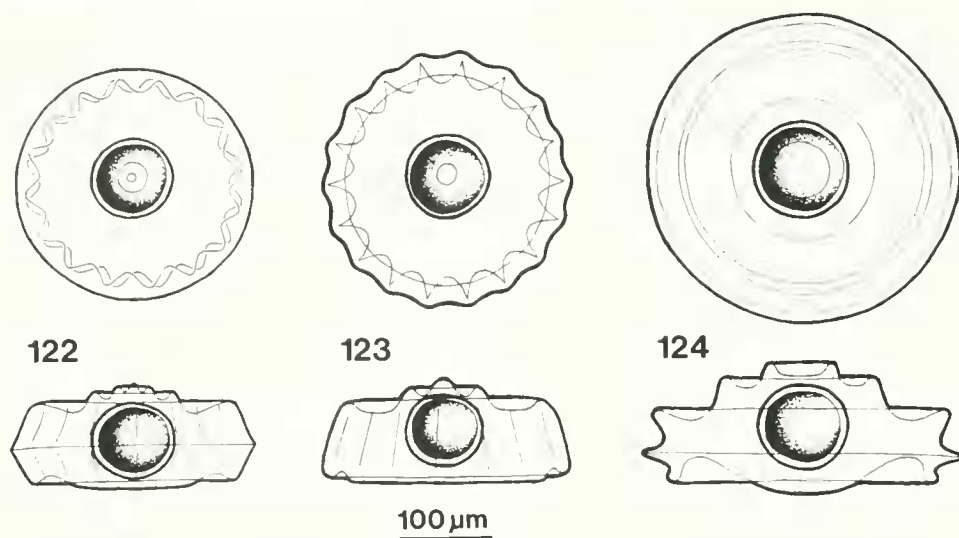
**Remarks:** Although shape and coloration are highly variable in this species as a whole, some geographical patterns can be distinguished. In southern Arabia the spire is a little taller, the shoulder more rounded, the peripheral keel less pronounced, and spiral sculpture on the dorsal surface is weaker or even absent (Figures 33, 69, 73). In the Persian Gulf and northern Oman there is a tendency to flattening of the spire, and development of heavy carinae at the shoulder and periphery, while the dark oblique lines become more numerous (Figures 31, 71, 74). Specimens from Kenya and Zanzibar are more rugose, sometimes with regular radial folds and slightly crenulate peripheral flange (Figures 34, 68). In the flattened and weakly shouldered specimens from the Seychelles (Figure 75) the lined color pattern is absent or occasionally present on the spire only. In typical specimens from the Mascarene Islands, Madagascar and Moçambique, the shoulder is scarcely marked and the color pattern is pronounced (Figures 30, 32).

The shell of this species is most likely to be confused with that of *P. isseli* (see Remarks on that species), which

→

**Figures 114–116.** Radulae of *Peasiella habei*. 114. Baten, Okinawa, Japan (flat view, shell D=3.2 mm). 115. Ma Liu Shi, Hong Kong (view at 45°, shell D=2.2 mm). 116. Gu Leng Yu, Xiamen, China (view at 45° from side, shell D=1.8 mm). 117. Radula of paratype of *Peasiella fasciata*, Turtle Bay, Cape Ferguson, Queensland, Australia (BMNH 1996273; view at 45°, shell D=2.1 mm). 118, 119. Radulae of *Peasiella isseli*. 118. Hurghada, Egypt (flat view, shell D=2.4 mm). 119. Hurghada, Egypt (view at 45°, shell D=3.0 mm). 120, 121. Two views (flat and at 45°) of radula of *Peasiella mauritiana*, Khor Hajar, Ras al-Hadd, Oman (shell D=3.6 mm). Scale bars = 20  $\mu\text{m}$ .





**Figures 122–124.** Egg capsules of *Peasiella* species. **122.** *Peasiella fasciata*, Cape d'Aguiar, Hong Kong. **123.** *Peasiella patula*, Changi Point, Singapore. **124.** *Peasiella habei*, Ma Liu Shi, Tolo Harbour, Hong Kong.

is endemic to the Red Sea; the two are only known to be sympatric close to the mouth of the Red Sea. Two other species, *P. infracostata* and *P. fuscopiperata*, can be found syntopically with *P. mauritiana*, and all three have diagnostic penial shapes. The shell of *P. infracostata* is always smooth above the periphery, and is thus easily distinguished from all ribbed and shouldered forms of *P. mauritiana*. However, examples of the latter from southern Oman and Yemen may lack ribs above the periphery, and if the shoulder angulation is poorly developed may be confused with *P. infracostata*. The basal ribs may then be useful; in *P. mauritiana* the outermost rib is the largest, but in *P. infracostata* the mid-basal rib is most prominent. Rare examples of *P. fuscopiperata* which have spiral sculpture above the periphery could be confused with this species, but lack the shoulder angulation.

#### ADDITIONAL NOTES ON OTHER SPECIES OF PEASIELLA

*Peasiella roepstorffiana* (Nevill, 1885)  
(Figures 142–145)

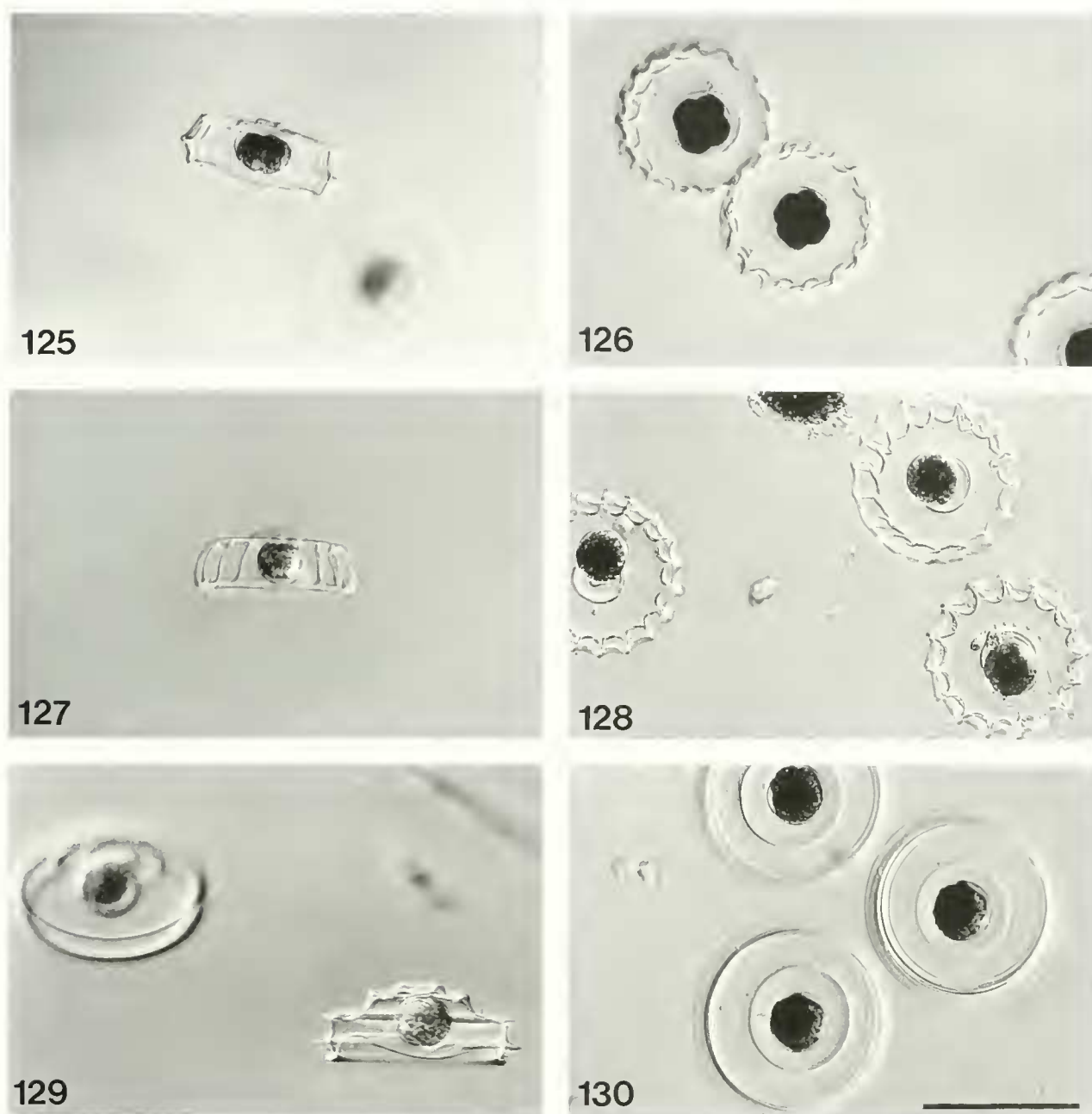
**Distribution:** *Additional records:* Indonesia: Ambon (NNML); Taiwan: Kending, Kaohsiang (BMNH); Yelihu, Taipei (BMNH). Japan: Kannon Saki, Ishigaki, Ryukyu Islands (BMNH).

**Remarks:** The range of this species is now extended from Hong Kong (Reid, 1989a, 1992) to Taiwan and the southernmost Ryukyu Islands (Figures 142, 144, 145), and also includes Ambon in Indonesia. A curious feature of this species is the apparent dimorphism of penial form; a mamilliform gland is present in material from Queensland, but not in specimens from Asia (Reid, 1989a). The absence of a penial gland has been confirmed in material from Ishigaki and Ambon. Additional

anatomical material has also been seen from Lautoka, Viti Levu, Fiji (BMNH); penial glands were found to be absent in two specimens, but in a third a rudimentary gland was present, with a cluster of subepithelial tissue but no reservoir or papilla. This supports the earlier suggestion that the penial dimorphism is indeed intraspecific. A similar case of geographical variation in presence or absence of a single penial gland has since been recorded in *Littorina kasatka* (Reid, 1996). The new Fijian material also supports the identification of the distinctive darkly tessellated shell from the eastern part of the range as merely a color variant of this species. Six additional radulae examined (Hong Kong, Singapore, Taiwan, Japan) each have 3 cusps on the outer marginal tooth, as recorded by Reid (1989a). The egg capsule of this species was described by Mak (1995) from Hong Kong; it is much larger than those capsules described here, 360–390  $\mu\text{m}$  in diameter, and similar in shape to that of *P. habei*, although without the two inner concentric rings on the upper surface.

*Peasiella conoidalis* (Pease, 1868)  
(Figures 138–141)

**Remarks:** Additional anatomical material of this species has been seen from Taiwan and Ishigaki, Ryukyu Islands (BMNH). The penial shape is the same as that illustrated by Reid (1989a), with a small and slender penial gland. Shells from these localities are often darker in color than those found elsewhere, with brown dots (or occasionally fine lines) in the spiral grooves above the periphery and strong brown marks in the folds between the peripheral crenulations (Figure 138). In some shells the pattern consists of 10–17 dark brown axial stripes (Figure 140). *Peasiella roepstorffiana* also occurs at these localities, and shells of the two are easily confused since both are yellow,



**Figures 125–130.** Egg capsules of *Peasiella* species. **125, 126.** *Peasiella fasciata*, Cape d'Aguilar, Hong Kong. **127, 128.** *Peasiella patula*, Changi Point, Singapore. **129, 130.** *Peasiella habei*, Ma Liu Shi, Tolo Harbour, Hong Kong. Scale bar = 200  $\mu$ m.

have radially plicate sculpture and peripheral crenulations (Figures 135, 141, 142, 145). They are separated by the following characters: in *P. conoidalis* the spiral grooves above the periphery usually contain small brown dots rather than continuous lines and the peripheral brown marks are weaker; the middle of the base of *P. conoidalis* shows 1–2 rows of small brown spots, whereas that of *P. roepstorffiana* is unmarked but for dark blotches on the underside of the peripheral keel and purple-tinged columella; the wide unsculptured area surrounding the umbilicus is characteristic of *P. roepstorffiana*; anatomically,

the single manilliform penial gland of *P. conoidalis* is lacking in *P. roepstorffiana* (note that these characters do not necessarily apply to the two species in other parts of their ranges, see Reid, 1989a). These two species are only occasionally found sympatrically elsewhere (e.g. Lizard Island, Australia; southeastern Papua New Guinea; Ambon, Indonesia; some islands in Fiji and the Philippines), since *P. conoidalis* has an oceanic distribution while that of *P. roepstorffiana* is more continental in character. An unidentified *Peasiella* species from Chichijima, in the Ogasawara (Bonin) Islands, illustrated by Fukuda (1993), is a

small, worn example of this species (specimen now in BMNH). *Peasiella conoidalis* has also now been recorded on the African mainland for the first time, from Tiwi Beach, Kenya (BMNH), where it occurred with *P. infracostata*, *P. fuscopiperata* and *P. mauritiana*. Another new record is from Ambon, Indonesia (NNML).

*Peasiella lutulenta* Reid, 1989

**Remarks:** This species is now recorded from Singapore (BMNH), where it appears to be rare. One of the five specimens found was a female with a mature pallial oviduct as well as a small penis (see Remarks on *P. habei* and *P. patula*). Two additional radulae examined each have 4 cusps on the outer marginal teeth, whereas Reid (1989a) found 3 cusps.

*Peasiella petiti* Le Renard, 1994

**Remarks:** This species from the Eocene of France was described and figured as *P. minuta* (Deshayes, 1824) by Reid (1989a); this name is preoccupied, and the species was renamed by Le Renard (1994).

## DISCUSSION

### SHELL VARIATION

Our reassessment of the taxonomy of *Peasiella* has not altered the earlier conclusion (Reid, 1989a) that the shell characters of these littorinids are unusually variable. Elsewhere in the family, species with likewise planktotrophic development do not normally show such conspicuous variation (e.g. Reid, 1986a, 1996). The variations in whorl outline and sculpture are most striking, since these characters are traditionally used to diagnose littorinid species. For example, in *P. infracostata* and *P. fuscopiperata* the periphery may be strongly keeled or smoothly rounded. In *P. isseli* and *P. mauritiana* the whorl profile may be almost flat or may develop a prominent carina at the shoulder. In *P. fuscopiperata*, *P. patula*, *P. habei* and *P. mauritiana* the surface above the periphery may be smooth or bear spiral ribs. Shell thickness is also variable, ranging from solid and opaque to thin and translucent in both *P. infracostata* and *P. fuscopiperata*. One sculptural character that is more useful for identification is the number and size of the ribs on the base. Many littorinids are conspicuously variable in shell color and pattern, and this is also the case in some *Peasiella* species, notably *P. isseli*. Nevertheless, we have found the number and arrangement of the oblique or spiral color bands to be one of the more useful characters for their identification. The cause and adaptive significance of shell variation in non-planktotrophic littorinids has been the subject of much research, but that of

the planktotrophic species is less well understood (reviews by McQuaid, 1996; Reid, 1996).

### ANATOMY

Throughout the family Littorinidae the shape of the penis is known to be one of the most useful taxonomic characters, and probably plays a role in species recognition in nature (e.g. taxonomic accounts and reviews by Reid, 1986a, 1989b, 1996). It was therefore surprising that the previous account of *Peasiella* (Reid, 1989a) concluded that penial shape was similar throughout the genus. All the six species for which anatomical material was then available showed a penis with a long filament and a single mamilliform penial gland (although in *P. roepstorffiana* the gland was found to be absent over much of the geographical range). The new material available to us in the present study has revealed that sympatric species do in fact frequently show diagnostic differences in penial form, particularly in the relative sizes of filament and penial gland.

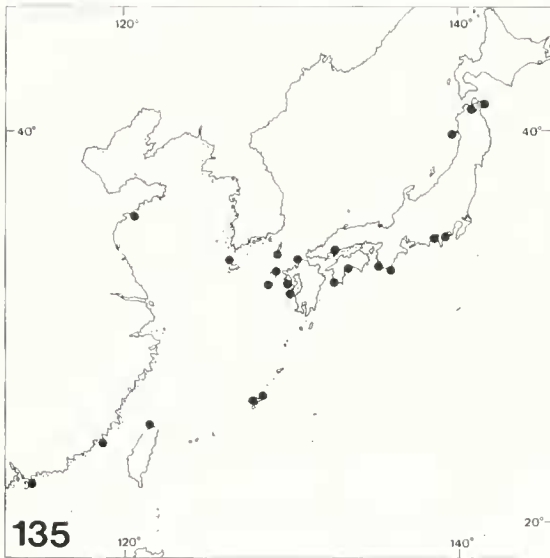
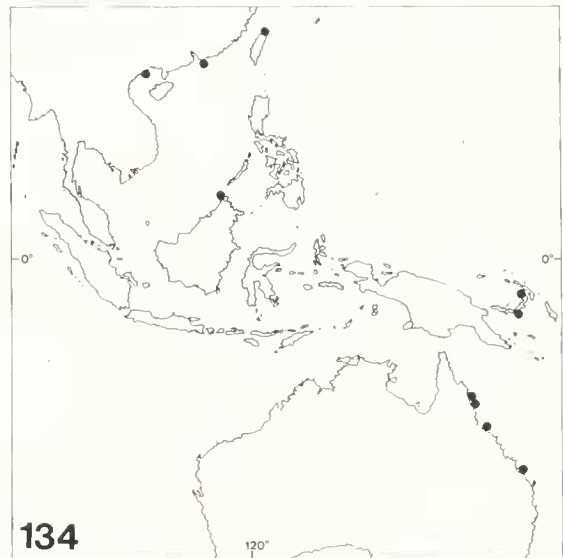
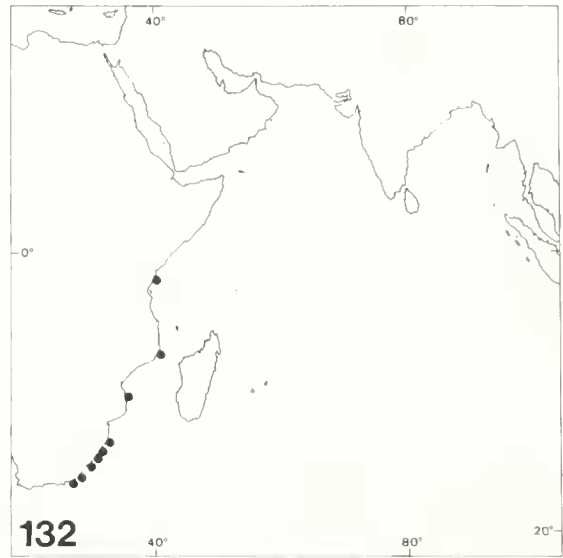
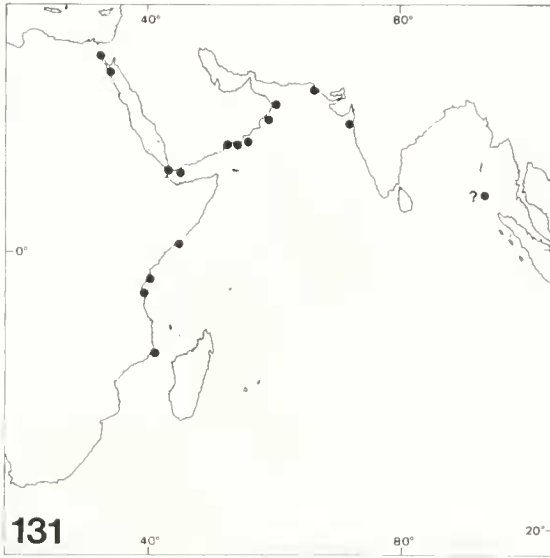
The gross morphology of the female reproductive system does not, however, show useful diagnostic characters. The arrangement of the loops of the egg groove through the glands of the pallial oviduct is the same in all 11 species of *Peasiella* (as illustrated by Reid, 1989a: figs. 57, 58, 65, 66). The copulatory bursa is apparently absent in six species, but this character is not useful for identification since it can be difficult to trace without histological preparation. Furthermore, in at least one littorinid, *Littorina saxatilis*, there is intraspecific variation in this feature, for the bursa is sometimes vestigial or absent in small, but mature, adults (Reid, 1996: 312).

The egg capsules of four *Peasiella* species have now been described (*P. habei*, *P. patula*, *P. fasciata*, herein; *P. roepstorffiana* in Mak, 1995). At least in *P. habei* the form of the capsule is constant over a wide geographical range, although there is some variation in size (see description of this species). These four species each show a unique capsule shape, and there is an almost twofold range of diameters among them. Similar interspecific variation is present in the genera *Nodilittorina* and *Littoraria* (reviews by Bandel & Kadolsky, 1982; Reid, 1986a, 1989b; Mak, 1995), although in most cases intraspecific variation is poorly known. The radial plication of the capsules of *P. patula* and *P. fasciata* has hitherto been described only in *Nodilittorina* species.

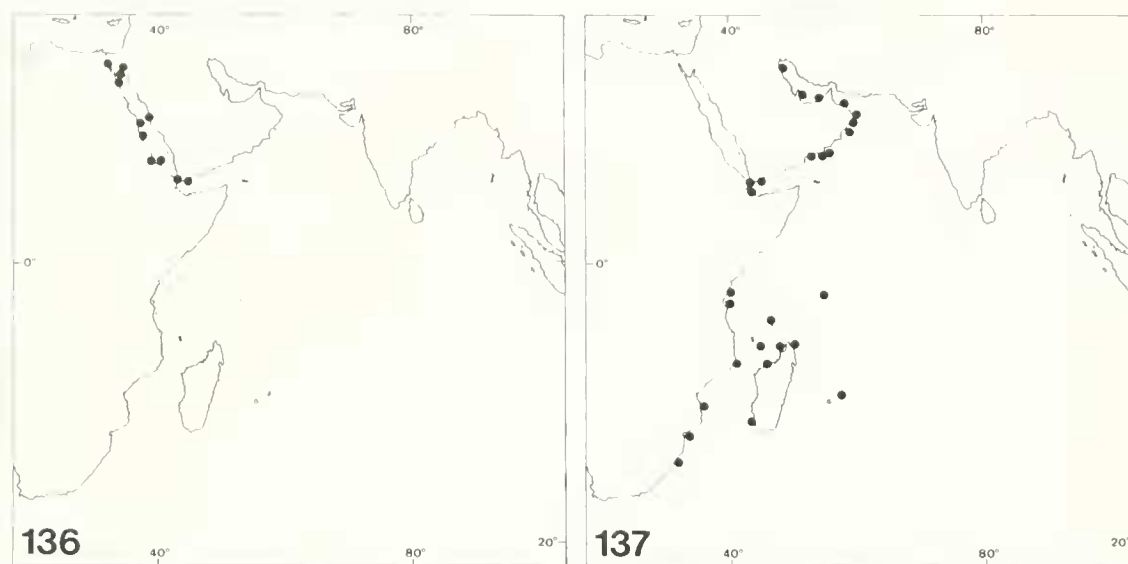
In general, the radula of littorinids is taxonomically useful for the diagnosis of generic groups (Reid, 1989b), but not at the species level (e.g. Reid, 1986a, 1996). As in the earlier study, we have found the radula of *Peasiella* species to be relatively uniform in the genus, showing interspecific variation only in the number of cusps on

→

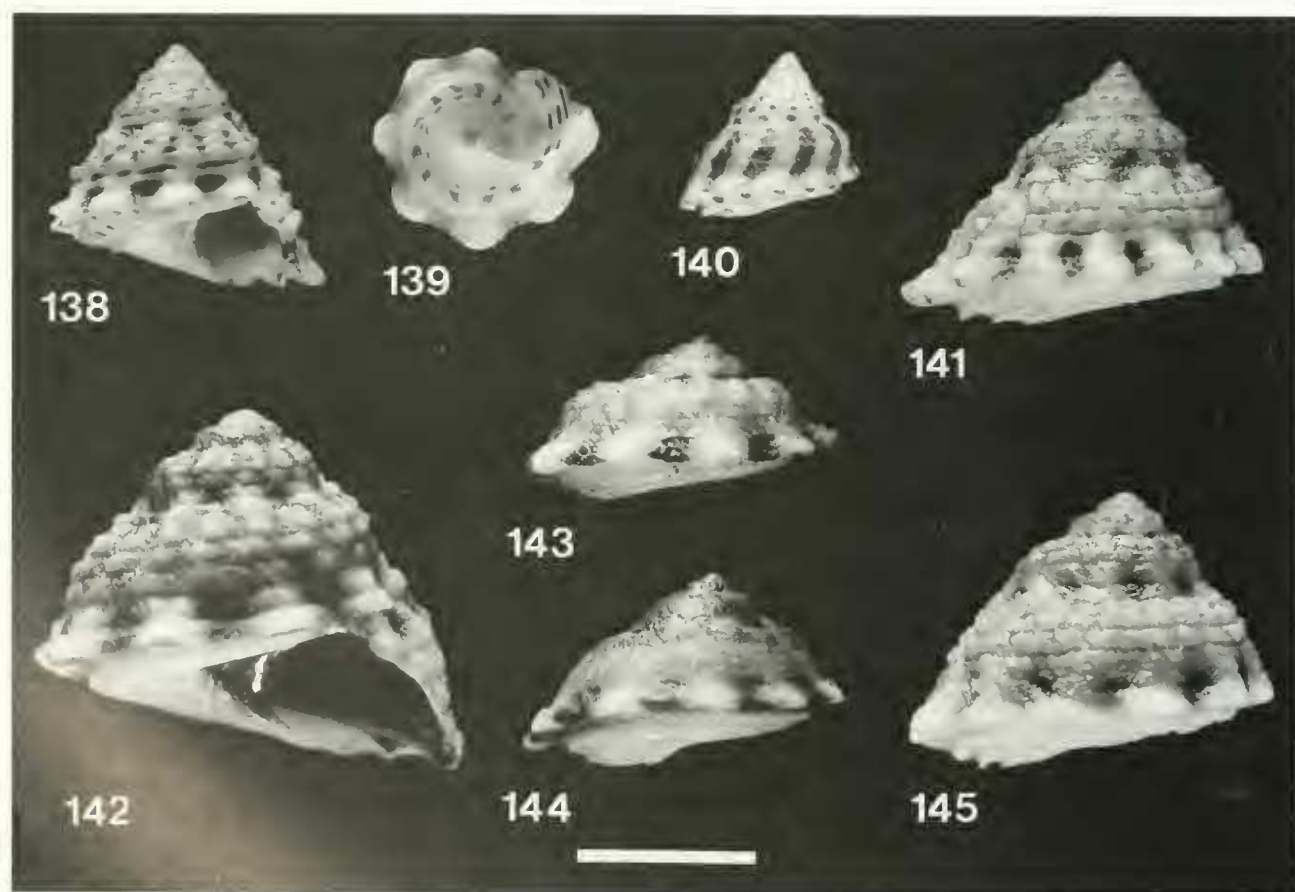
**Figures 131–135.** Distribution maps of *Peasiella* species, compiled from records listed in text. **131.** *Peasiella infracostata* **132.** *Peasiella fuscopiperata* **133.** *Peasiella patula* **134.** *Peasiella fasciata* **135.** *Peasiella habei*.







Figures 136, 137. Distribution maps of *Peasiella* species, compiled from records listed in text. 136. *Peasiella isseli*. 137. *Peasiella mauritiana*.



Figures 138–141. *Peasiella conoidalis*, Kending, Kaohsiang, Taiwan (BMNH 1996398). 142–145. *Peasiella roepstorffiana* 142. Kannon Saki, Ishigaki, Japan (BMNH 1996399) 143. Ma Lin Shi, Hong Kong (BMNH 1996400). 144. Yehlin, Taipei, Taiwan (BMNH 1996401) 145. Kending, Kaohsiang, Taiwan (BMNH 1996402). Scale bar = 2 mm.

the outer marginal tooth, and in the development of basal denticles on the rachidian tooth.

#### PHYLOGENY AND BIOGEOGRAPHY

The phylogenetic relationships of *Peasiella* within the Littorinidae remain uncertain. In the morphological phylogenetic analysis of Reid (1989b), the genus appeared as the sister-taxon of *Mainwaringia* in the consensus of all equally parsimonious trees; however, no unique synapomorphy for these two taxa was found. Anatomically, they are similar in their penial form (single mamilliform gland and closed sperm duct), pallial oviduct loops (although these are slightly more complex in *Mainwaringia*, Reid, 1986b) and egg capsule shape (compare Reid, 1990:fig. 3j with Mak, 1995: fig. 2d), but some of these resemblances may be plesiomorphic. They are so different in their shell and opercular shape, radular teeth and in the unique hermaphroditism of *Mainwaringia*, that a close relationship might seem unlikely. Nevertheless, preliminary molecular data offers some support for their sister-group relationship, and is currently under investigation (R. H. Thomas, pers. comm.).

Morphological features do not provide sufficient information for a cladistic analysis at the species level, and in the absence of an unequivocal sister-group the polarities of the few available characters are doubtful. The five species confused by Reid (1989a) under the name *P. infracostata* (*P. infracostata*, *P. fuscopiperata*, *P. patula*, *P. habeii*, *P. fasciata*) are a possible clade, showing some similarity in shell form (tendency to reduction of peripheral keel and spiral ribs, presence of spiral color bands), and in radular cusps (4–8 cusps on outer marginal tooth, except 3–4 in *P. patula*; cf. 3–4 in all remaining species).

Four probable pairs of sister-species can be suggested. *Peasiella infracostata* and *P. fuscopiperata* are closely similar in shell characters; both lack a copulatory bursa, and radular cusps are similar. Their geographical distributions are known to overlap only between Mozambique and Kenya, which might suggest an allopatric mode of speciation followed by limited secondary contact. These two have strikingly dissimilar penial shapes, as would be predicted if this were either an isolating or species-recognition mechanism (Reid, 1996). A second likely sister-species pair is *P. isseli* and *P. mauritiana*. Again these are similar in shell characters, but differ in penial shape. These are almost completely allopatric; *P. isseli* is restricted to the Red Sea, while *P. mauritiana* occurs widely in the Indian Ocean and Persian Gulf, and they overlap only in the vicinity of Aden and at the mouth of the Red Sea. While endemism in the Red Sea fauna is high in some groups, among mollusks it is generally low (Sheppard *et al.*, 1992). During the substantial falls in sea level produced by Pleistocene glaciation, the Red Sea became hypersaline, and recolonization from the Arabian Sea has occurred only since the Holocene transgression. Speciation in the Red Sea may therefore be a

recent phenomenon. At present, the currents at the mouth of the Red Sea do not appear to prevent passage of planktonic larvae, but the cold upwelling on the southern Arabian coast during the summer months may cause a partial isolation of the Red Sea from the Arabian Sea and Indian Ocean (Sheppard *et al.*, 1992). The third likely pair is *P. habeii* and *P. fasciata*, which both belong in the 'infracostata group'. These are known to overlap only between Hong Kong and Taiwan, and show a slight but consistent difference in penial shape. Finally, *P. conoidalis* and *P. tantilla* may be sister-species. Their radula, oviduct and penis are identical, shells are similar in sculpture, and both occur only on oceanic islands (Reid, 1989a). The former is widespread throughout the Indo-West Pacific, whereas the latter is restricted to the Hawaiian Islands, suggesting a case of speciation by peripheral isolation. The species status of *P. tantilla* is based only on its distinct shell. The two are not known to occur sympatrically and, assuming that penial shape is an isolating mechanism, there has presumably been no selection for its divergence.

#### ACKNOWLEDGMENTS

This work was carried out while Y-MM was in receipt of a post-doctoral fellowship from the Croncher Foundation, Hong Kong. We thank E. Glover and J. D. Taylor (BMNH), S-Y. Chan (Singapore), H.L. Strack (Dordrecht, The Netherlands), Y. Shikano, (Tokyo) and E. Platts (Winchester, U.K.) for providing specimens. For assisting Y-MM with field collecting we thank K. S. Tan (National University of Singapore), Fu-xue Li (Xiamen University), C. K. Tseng (Institute of Oceanography, Qingdao), Huang Shong (National Taiwan Normal University), Michael Hin-kin Mok (National Sun Yat-sen University, Taiwan), S. Yamato and S. Ohgaki (Kyoto University, Shirahama), Y. Takada (Ishigaki Tropical Station) and all their colleagues. For providing loans of material we are grateful to P. Bouchet (MNHN), H. Dekker (The Netherlands), H. Fukuda (Tokyo Metropolitan University), R. N. Kilburn (NM), I. Loch (AMS), R. Moolenbeek (ZMA) and J. Pickering (OUM). For their expert photography of shells we thank H. Taylor and N. Hayes (BMNH). P. York (BMNH) kindly assisted with the photomicroscopy of egg capsules. We appreciate the helpful comments of two anonymous referees.

#### LITERATURE CITED

- Amio, M. 1963. A comparative embryology of marine gastropods, with ecological consideration. *Journal of the Shimomoseki University of Fisheries* 12:229-358.
- Audouin, V. 1826. Explication sommaire des planches de mollusques de l'Égypte et de la Syrie, publiée par Jules César Savigny. *Description de l'Égypte. Histoire Naturelle* 1(4): 7-56.
- Bandel, K. 1974. Studies on Littorinidae from the Atlantic. *The Veliger* 17(2):92-114

- Bandel, K. and D. Kadolsky. 1952. Western Atlantic species of *Nodilittorina* (Gastropoda: Prosobranchia): comparative morphology and its functional, ecological, phylogenetic and taxonomic implications. *The Veliger* 25(1):1-42.
- Bauer, B., P. Fioroni, I. Ide, S. Liebe, J. Oehlmann, E. Stroben and B. Watermann. 1995. TBT effects on the female genital system of *Littorina littorea*: a possible indicator of tributyltin pollution. *Hydrobiologia* 309:15-27.
- Bosch, D. T., S. P. Dance, R. G. Moolenbeek and P. G. Oliver. 1995. *Seashells of eastern Arabia*. Motivate Publishing, Dubai. 296 pp.
- Bouchet, P. and F. Danrigal. 1952. Napoleon's Egyptian campaign (1798-1801) and the Savigny collection of shells. *The Nautilus* 96(1):9-24.
- Choe, B. L. 1992. Illustrated encyclopaedia of fauna and flora of Korea, Vol. 33: Mollusca (II). Ministry of Education, Republic of Korea.
- Choe, B. L. and J. K. Park. 1993. Seven unrecorded mesogastropodous species (Gastropoda: Mollusca) from Korean waters—superfamilies Littorinacea, Tornacea, Rissoinacea, and Cerithiacea. *Korean Journal of Malacology* 9:17-26.
- Dautzenberg, P. 1929. Mollusques testacés marins de Madagascar. *Faune des Colonies Françaises* 3:322-636.
- Franç, A. 1956. Résultats scientifiques des campagnes de la *Calypso*. II.- Campagne 1951-1952 en Mer Rouge. 9. Mollusques marins. *Annales de l'Institut Océanographique* 32:19-60.
- Fukuda, H. 1993. Marine Gastropoda (Mollusca) of the Ogasawara (Bonin) Islands. Part 1: Archaeogastropoda and Neotaenioglossa. *Ogasawara Research* 19:1-86.
- Fukuda, H., Mashino, K. & Sugimura, T. 1992. A review of the molluscan fauna of Yamaguchi Prefecture, Western Japan. Yamaguchi Museum.
- Habe, T. 1956. The floating egg capsules of the Japanese periwinkles (Littorinidae). *Venus* 19(2):117-121.
- Habe, T. 1964. Shells of the western Pacific in color, Vol. 2. Hoikusha, Osaka, 233 pp.
- Habe, T. 1984. *Peasiella roepstorffiana* (Nevill) and *P. gaidoi* (Montrouzier). *Chiribotan* 15:11-12.
- Higo, S. 1973. A catalogue of molluscan fauna of the Japanese Islands and the adjacent area. 61 p.
- Higo, S. and Goto, Y. 1993. A systematic list of molluscan shells from the Japanese Islands and the adjacent area. *Ent Malacological Publishers, Yao, Osaka*, 693+145 pp.
- Issel, A. 1869. *Malacologia del Mar Rosso*. Pisa.
- Lamy, E. 1938. Mission Robert Ph. Dollfus en Égypte. VII. Mollusca Testacea. *Mémoires de l'Institut d'Égypte* 37:1-59.
- Le Renard, J. 1994. Révision des mollusques paléogènes du bassin de Paris. I. Rectifications de nomenclature d'espèces. *Cossmanniana* 3:35-40.
- Mak, Y.-M. 1995. Egg capsule morphology of five Hong Kong rocky shore littorinids. *Hydrobiologia* 309:53-59.
- Mastaller, M. 1979. Beiträge zur Faunistik und ökologie der Mollusken und Echinodermen in den Korallenriffen bei Agaba, Rotes Meer. Ph.D. thesis, Ruhr-Universität Bochum, 344 pp.
- McQuaid, C. D. 1996. Biology of the gastropod family Littorinidae. I. Evolutionary aspects. *Oceanography and Marine Biology Annual Review* 34:233-262.
- Melville, J. C. and R. Standen. 1901. The Mollusca of the Persian Gulf, Gulf of Oman, and Arabian Sea, as evidenced mainly through the collections of Mr. F. W. Townsend, 1893-1900, with descriptions of new species. *Proceedings of the Zoological Society of London* 1901(2):327-460.
- Moazzo, P. G. 1939. Mollusques testacés marins du canal de Suez. *Mémoires de l'Institut d'Égypte* 35:1-283.
- Mori, K., S. Nishihama and M. Tanaka, M. 1955a. Community structure of a rocky shore in Tsuji-shima Island, Amakusa. III. The analysis of relationships between distribution of organisms and micro-topographical conditions using small quadrat. *Publications of the Amakusa Marine Biological Laboratory* 5:43-63.
- Mori, K., M. Tanaka and S. Nishihama. 1955. Community structure of a rocky shore in Tsuji-shima Island, Amakusa. H. Vertical distribution of dominant species and its zonation pattern. *Publications of the Amakusa Marine Biological Laboratory* 5:27-41.
- Nevill, G. 1855. Hand list of Mollusca in the Indian Museum, Calcutta. Part 2. Indian Museum, Calcutta, 306 pp.
- Ohtsuka, S. and E. Yoshioka. 1955. A preliminary note on the pelagic eggs of marine invertebrates. *Special Publications of the Mukaishima Marine Biological Station* 1955:225-235.
- Okutani, T. 1986. Colored illustrations of living things: molluscs. Sekaibunkasha Co., Tokyo.
- Oyama, K. and Y. Takemura. 1961. *The molluscan shells*, Vol. 5. Resources Exploitation Institute, Tokyo.
- Pallary, P. 1926. Explication des planches de J. C. Savigny. *Mémoires de l'Institut d'Égypte* 11:1-138.
- Reid, D. G. 1986a. The littorinid mollusks of mangrove forests in the Indo-Pacific region: the genus *Littoraria*. *British Museum (Natural History)*, London, xv+225 pp.
- Reid, D. G. 1986b. *Mainucaringia* Nevill, 1855, a littorinid genus from Asiatic mangrove forests, and a case of protandrous hermaphroditism. *Journal of Molluscan Studies* 52:225-242.
- Reid, D. G. 1988. The genera *Bembicium* and *Risellopsis* (Gastropoda: Littorinidae) in Australia and New Zealand. *Records of the Australian Museum* 40:91-150.
- Reid, D. G. 1989a. Systematic revision of the Recent species of *Peasiella* Nevill, 1855 (Gastropoda: Littorinidae), with notes on the fossil species. *The Nautilus* 103(2):43-69.
- Reid, D. G. 1989b. The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London. Series B* 324:1-110.
- Reid, D. G. 1990b. A cladistic phylogeny of the genus *Littorina* (Gastropoda): implications for evolution of reproductive strategies and for classification. *Hydrobiologia* 193:1-19.
- Reid, D. G. 1992. The gastropod family Littorinidae in Hong Kong. *In*: Morton, B. (ed.). *Proceedings of the Fourth International Marine Biological Workshop: The marine flora and fauna of Hong Kong and southern China III*. Hong Kong University Press, Hong Kong, pp. 187-210.
- Reid, D. G. 1996. *Systematics and Evolution of Littorina*. Ray Society, London. x+463 pp.
- Reid, D. G. and J. B. Geller. 1997. A new ovoviviparous species of *Tectarius* (Gastropoda: Littorinidae) from the tropical Pacific, with a molecular phylogeny of the genus. *Journal of Molluscan Studies* 63(2):207-233.
- Rosewater, J. 1972. The family Littorinidae in the Indo-Pacific. Part II. The subfamilies Tectariinae and Echiniminae. *Indo-Pacific Mollusca* 2:507-533.
- Savigny, J. C. 1817. *Description de l'Égypte. Histoire Naturelle. Planches*, Vol. 2. Imprimerie Royale, Paris.
- Sheppard, C., A. Price and C. Roberts. 1992. *Marine ecology*

- of the Arabian region. Patterns and processes in extreme tropical environments. Academic Press, London, 359 pp.
- Tanaka, M., K. Mori, S. Nojima, T. Kikuchi, T. Shibata, T. Nishino and K. Omori. 1985. Community structure of a rocky shore in Tsuji-shima Island, Amakusa. I. Horizontal and vertical distribution pattern of common animals. Publications of the Amakusa Marine Biological Laboratory 8: 1-26.
- Tillier, L. and A. Bavay. 1906. Les mollusques testacés du canal de Suez. Bulletin de la Société Zoologique de France 30: 170-181.
- Tokioka, T. 1950. Droplets from the plankton net V. New names for egg capsules of littorinid gastropods. Publications of the Seto Marine Biological Laboratory 1:151-152.
- Tryon, G. W. 1887. Manual of conchology, Vol. 9, Philadelphia, 488 pp.
- Turton, W. H. 1932. The marine shells of Port Alfred, South Africa. Oxford University Press, Oxford, 331 pp.
- Viader, R. 1951. New or unrecorded shells from Mauritius and its dependencies. Mauritius Institute Bulletin 3:127-153.
- Yamamoto, G. and T. Habe. 1962. Fauna of shell bearing mollusks in Mutsu Bay. Bulletin of the Biological Station of Asamushi, Tohoku University 11:1-20.